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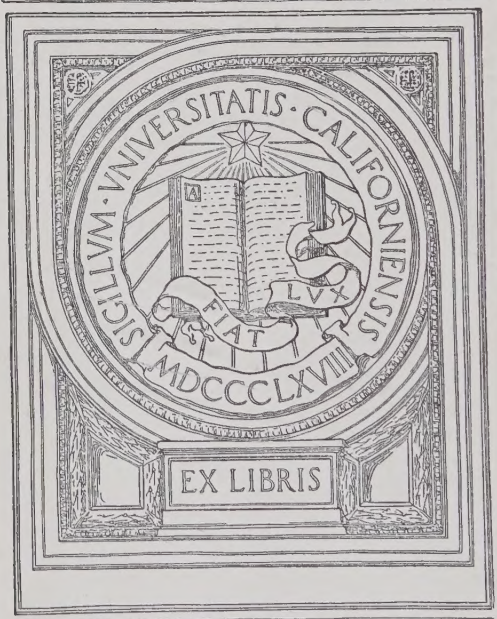

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A TREATISE ON THE BRITISH FRESHWATER ALGAE

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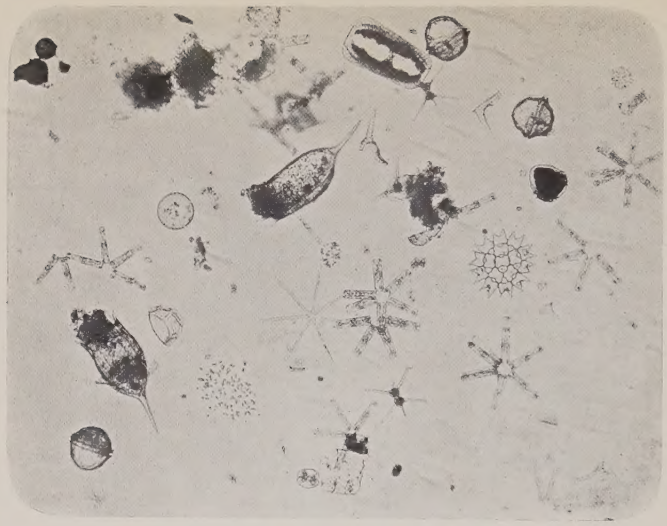

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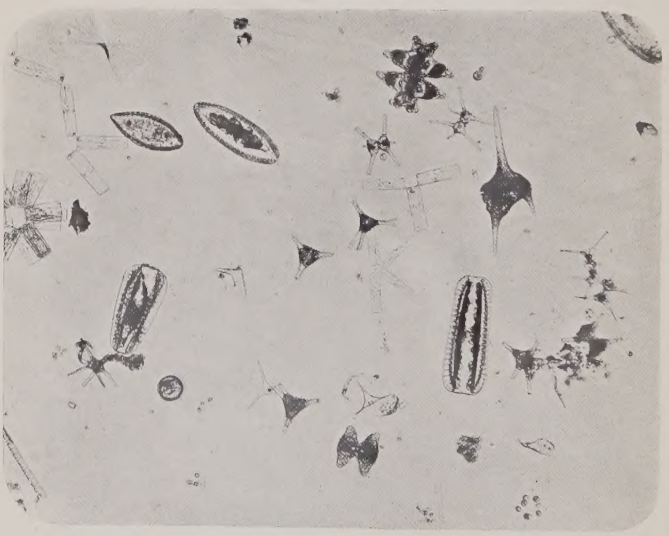

Plankton from Loch Ruar, Sutherland (× 100).

WILLIAM A. SETCHELL

A TREATISE
ON THE
BRITISH FRESHWATER ALGAE

IN WHICH ARE INCLUDED ALL THE *PIGMENTED PROTOPHYTA* HITHERTO FOUND IN BRITISH FRESHWATERS

by

THE LATE
G. S. WEST, M.A., D.Sc., F.L.S., A.R.C.S.
Professor of Botany at the University of Birmingham

NEW & REVISED EDITION
IN GREAT PART REWRITTEN

by

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PREFACE TO THE SECOND EDITION

NEARLY a quarter of a century has elapsed since the publication of the first edition of "British Freshwater Algae," and this moreover covers a period in which all branches of botanical science have been pursued with great vigour. Our knowledge of the Algae and related organisms has advanced very considerably during that time and, thanks especially to the fundamental work of G. S. West, the British freshwater algal flora has been materially enriched, both by the description of new genera and species and by the discovery of forms already known from other parts of the world. When therefore I was requested by the Syndics of the Cambridge University Press to undertake the preparation of a new edition of West's work which should not appreciably exceed the dimensions of the earlier one, I felt that this could only be accomplished by practically rewriting the greater part of the book. While I hope to have preserved the essential character of the former work, very extensive changes have been made to bring it into line with the present-day outlook. A considerable amount of the matter in the earlier edition has had to be omitted, but I have retained practically in their entirety the data on occurrence and distribution of British freshwater Algae (mainly rendered in small type) that G. S. West compiled from his own unrivalled experience. The generic descriptions, except where it was necessary to bring them up to date or to amplify them, have also been little modified.

As indicated more fully in the introductory section, it is no longer thought feasible to separate the Algae from the pigmented Flagellata, and the scope of this volume has therefore been extended to include all the holophytic Protophyta (incl. Peridinieae) that have been found in the British Isles. The colourless forms have however been omitted, except in a few cases in which a very close relationship with pigmented types is apparent, and the large classes of colourless Flagellata recognised by Senn are not considered here. In general the treatment of the different

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classes has been confined to the British representatives, but some mention of others likely to be found in this country has frequently been made, either because their description was necessary for the clear understanding of the characters of a class or in order to draw attention to them, so that they might be sought for.

An attempt has been made to give a more detailed oversight of the essential features of each class (also of each group in the case of the Isokontae) than was done in the first edition. This has rendered possible a briefer consideration of the individual families whose description is mostly confined to a few lines. Moreover the keys for the determination of genera have been concentrated and placed at the beginning of the systematic treatment of each class or larger group. It is believed that this will afford greater facility in determination. The introductory sections to the different groups and classes will, if read in continuity, constitute an introduction to the study of freshwater Algae for beginners, especially if supplemented by occasional reference to the subsequent generic descriptions. In order to save space the latter are given in diagnostic form and a few very obvious contractions are used. In the general survey which follows the description of each genus, some attempt has been made (except in the case of the larger genera) to indicate the essential characters of the species mentioned. All measurements, unless otherwise stated, are given in terms of μ.

Literature has been cited to a very much greater extent than in the first edition, and under each genus are enumerated any important papers relating to it. The citation of literature is in no way exhaustive, but it is believed that no important paper, published up to the end of 1925, has been omitted. A certain number of papers and books, to which frequent reference has had to be made, are indicated only by the author's name and the year of publication, and a list of these will be found at the end of the book. It may be well to state that the works in question are not necessarily more important than many which are cited in the main body of the book.

The present work contains the description of 62 genera that were not included in the earlier edition. The majority of the

illustrations in the latter have been retained, but a few have been replaced and a considerable number of new blocks added. There is a figure for every British freshwater algal genus, and in the case of the larger genera several species are usually figured. It has been a matter for regret that lack of space has prevented more than a very cursory consideration of the numerous contributions on algal ecology and biology.

In conclusion I wish to acknowledge the help and inspiration afforded by Oltmanns' "Morphologie und Biologie der Algen." G. S. West's Handbook, and Pascher's "Süsswasserflora" have also been abundantly consulted. I am much indebted to my colleague, Dr Nellie Carter, with whom I have discussed many difficult points, to my fellow-worker, Miss F. Rich, who has read the proofs throughout, and to my wife for the arduous task of preparing the new blocks of illustrations.

F. E. FRITSCH

Dorking, Surrey
March 6th, 1926

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ABBREVIATIONS

All measurements, except where otherwise stated, are given in terms of μ (one-thousandth of a millimetre). The following abbreviations are used in the text: aplanosp. = aplanospore; aquat. = aquatic; asex. = asexual; auxosp. = auxospore; azygosp. = azygospore; br. = breadth; Brit. = British; chloropl. = chloroplast; chromat. = chromatophore; conjug. = conjugation; contr. vac. = contractile vacuole; diam. = diameter; div. = division; fil. = filament; intercell. sp. = intercellular spaces; l. = length; longit. = longitudinal; multipl. = multiplication; opp. = opposite; pyren. = pyrenoid; reprod. = reproduction; sex. = sexual; sp. = species; terrestr. = terrestrial; transv. = transverse; trich. = trichome; unicell. = unicellular; vac. = vacuole; zoosp. = zoospore; zygosp. = zygospore.

INTRODUCTION[1]

History of the Study of British Freshwater Algae

One of the earliest attempts to bring together all that was then known concerning British Freshwater Algae was Dillwyn's "British Confervae" which appeared in 1809, and hardly any further advance was made in this country until the publication in 1845 of Hassall's "History of British Freshwater Algae." About this time two very important works were commenced on the continent, one being Kützing's "Tabulae Phycologicae," the first part of which was issued in 1846, and the other Rabenhorst's "Flora Europaea Algarum," published between 1864 and 1868. Naegeli's "Gattungen einzelliger Algen" (1849) helped materially to advance our knowledge of the unicellular forms. Ralfs' "British Desmids" appeared in 1848, but for the next thirty years Henfrey, Hicks, and Archer were almost the only contributors to the literature of British freshwater Algae, the publications of Archer being very numerous and most valuable. From 1882 to 1884 Cooke issued his "British Freshwater Algae" and in 1887 Wolle's "Freshwater Algae of the United States" appeared, but it can scarcely be said that either of these works contributed much to further knowledge of the Algae. The study of Diatoms was materially advanced during this period by the publication, between 1853 and 1856, of Smith's "Synopsis of the British Diatomaceae" and Van Heurck's "Synopsis des Diatomées de Belgique" (1880–85).

The last two decades of the nineteenth century saw a great increase in the investigation of freshwater Algae, particularly by continental workers such as Wille, Wittrock, Nordstedt, Bornet, Thuret, Lagerheim, Klebs, Hansgirg, Schmidle, Borzi, Chodat, Borge, Lemmermann, and others. In Britain, Bennett and Roy dealt with the algal flora of certain districts, and towards the end of this period W. West, the father, and G. S. West, the son, commenced the publication of the series of memoirs on the freshwater Algae of many parts of the British Isles (as well as of other regions) that constitute a model of what such researches should be and have rightly led to their names being ranked amongst the foremost workers on the taxonomy of freshwater

[1] Literature is quoted by reference to the author's name and the place of publication, except in the case of a few papers and books which are cited by giving the author's name and year only; a list of these will be found at the end of the present work.

Algae. The study of the latter received a further impetus through the publication in 1902 of Chodat's "Algues vertes de la Suisse," of the first edition of the present work by G. S. West in 1904, and of Oltmanns' "Morphologie und Biologie der Algen" in the same year. W. and G. S. West's "Monograph of the British Desmidiaceae," of which the first volume was issued in 1904, had a far-reaching influence on the study of the large group with which it deals. De Toni's "Sylloge Algarum," commenced in 1889, served the useful purpose of giving an oversight of the numerous genera and species that were at that time already known.

In the present century great advances have been made in the investigation of freshwater Algae in many parts of the world, and in particular attention has been paid to their biology and ecology. The study of freshwater phytoplankton belongs almost entirely to this period. Space does not admit of mentioning the innumerable younger workers who now occupy the field and have already contributed much to our knowledge of freshwater Algae. Amongst those of Great Britain may be mentioned Nellie Carter, Hodgetts, and Griffiths; amongst others Pascher, Printz, Strom, Comère, Allorge, Heering, Geitler, B. Schröder, G. M. Smith, etc. Two important works that have appeared during this period are Pascher's "Süsswasserflora Deutschlands, Österreichs, und der Schweiz" and G. S. West's volume on Algae in the Cambridge Botanical Handbooks (1916).

The researches of the last 40 years have not only led to the discovery of many new genera and species and the elucidation of the life-histories and mode of life of many forms, but in addition a great deal has been accomplished in clearing up the synonymy of these plants. It may be doubted if 25 per cent. of the British freshwater Algae could be identified with certainty from Cooke's book, and Wolle's American publication would be of little or no assistance. The widespread assumptions as regards polymorphism of Algae, based upon very inadequate observations (Borzi, Hansgirg, etc.), that were current in the eighties of the last century, have been largely abandoned[1]. In particular it is now quite clear that there exist a large number of simple and colonial Algae (such as are comprised in the groups Volvocales, Chlorococcales, Chroococcales, etc.) that are quite independent of the higher filamentous types, though certain stages in the life-history of the latter may occasionally markedly resemble some of the former. Moreover, even where the independence of a simple form is in doubt, that constitutes no

[1] cf. Klebs, 1896, p. 172; West, 1899, p. 52; Oltmanns, Morph. u. Biol. d. Algen, III, 1923, p. 69.

reason why, until its assignation to some other is fully established, it should be neglected and left out of consideration. A carefully described and figured algal form always marks a contribution to our knowledge of the group, no matter whether it be subsequently found to represent merely a stage in the life-cycle of some other species.

The classification of the Algae has undergone manifold changes and, although we are doubtless far from possessing a natural system, great strides in that direction have been made in the last 30 years. The most marked advance was the elaboration of a theory of the origin of the Algae from a flagellate ancestry, which emanated from Sweden and may be identified with the names of Bohlin and Luther[1]. In this country this theory was first clearly expounded by F. F. Blackman[2] in 1900, and this was followed in 1902 by the publication of a revised classification of the Green Algae by Blackman and Tansley[3]. The point of view initiated by this theory has given a great stimulus to the investigation of the simpler unicellular and colonial Algae as well as of the pigmented Flagellates themselves, and the advance in our knowledge has been particularly noticeable during the last fifteen years, thanks especially to the important work of Pascher[4]. It may be doubted whether at the present day the distinction between Flagellates and Algae is still a tenable one, since it is evident that there are a large number of phyla of pigmented Protophyta that, commencing with simple flagellate forms, have advanced to a more or less high stage of algal organisation (cf. p. 19). For this reason all the pigmented Protophyta have been included in the present edition.

In the subsequent matter a general acquaintance with plants is assumed, such as can be obtained from any elementary text-book dealing with botany. The student is advised to gain familiarity with the general characteristics of the structure and reproduction of a few of the commoner freshwater Algae, such as can be obtained from a perusal of Scott's "Structural Botany" or of Fritsch and Salisbury's "Introduction to the Structure and Reproduction of Plants."

[1] Luther, Bih. K. Sv. Vet.-Akad. Handl. XXIV, 1899, Afd. 3, No. 13, p. 14 et seq.; Bohlin, Utkast till de gröna Algernas och Arkegoniaternas Fylogeni, Upsala, 1901.

[2] Blackman, Ann. of Bot. XIV, 1900, p. 647.

[3] New Phytol. I, 1902, p. 17, etc.

[4] cf. especially Pascher, 1914, 1918 and 1921.

Occurrence and Distribution of Freshwater Algae

Algae are universal in their occurrence, no moist situation being without some type of Alga. They are found in and on damp earth, on rocks, walls, palings, tree-trunks, in rain-tubs, etc.; they are met with in all kinds of running water, from the torrent, waterfall, and cataract to the slowest river. They are most abundant however in still waters, occurring in quantity in pools, ditches, and lakes.

They are found either floating at the surface, simply immersed in the water, or attached to submerged stones or to larger aquatic plants as epiphytes. The larger Algae are often conspicuous as green or blue-green slimy masses (so-called pond-scums) forming a surface scum on ponds, ditches, etc., or take the shape of long green tresses attached to the rocks and stones of rivers. Rocks over which water is constantly dripping possess at times quite a characteristic flora comprising many of the more uncommon Algae. If such rocks present wet vertical faces, they are often covered with thick leathery patches or gelatinous masses, which exhibit a great variety of colours and usually consist of a mixture of blue-green Algae (Myxophyceae). A few forms (*Botrydium*, some species of *Vaucheria*) are customarily found on the damp mud left after the water recedes around the edge of a pond.

A number of Algae live as endophytes within the bodies of other organisms, vegetable or animal. Some of these are mere "space-parasites," obtaining shelter by occupying the intercellular spaces of various plants (e.g. *Chlorochytrium* within species of *Lemna* (fig. 26, D); *Anabaena Azollae* within *Azolla*, *Nostoc* in species of *Anthoceros*, etc.). In other cases however there is a symbiotic relation with the host, which not only affords shelter but also provides part of the food-supply, probably receiving in its turn some of the products of photosynthesis of the Alga. This is the case in Lichens, where a Fungus lives symbiotically with Algae such as *Trebouxia* (p. 107), *Trentepohlia*, *Nostoc*, *Scytonema*, etc. The "green cells" found within such animals as *Hydra viridis*, *Paramoecium*, *Ophrydium*[1], etc., as well as in freshwater Sponges, are due to species of *Chlorella*[2]. Other modes of occurrence of Algae are illustrated by the genus *Foreliella* whose threads perforate the substance of the valves

[1] Large green gelatinous masses belonging to this genus often occur in huge quantities in ponds and lakes.

[2] A similar occurrence of "green cells" within freshwater snails has been recently brought to the notice of the writer by Prof. A. E. Boycott, F.R.S.

of the freshwater Mussel (*Anodonta*[1]), and *Trichophilus*, which inhabits the superficial layers of the hairs of the Sloth (*Bradypus*)[2].

Many of the most beautiful Algae are exceedingly minute and occur in quantity in situations which are not at first obvious and are only found by experience. They occur embedded in a thin mucus surrounding the stems and leaves of submerged plants, such as *Utricularia*, *Myriophyllum*, *Nymphaea*, *Nuphar*, *Potamogeton*, *Scirpus fluitans*, *Isoetes*, etc. Many submerged Bryophytes, such as *Sphagnum contortum*, *S. plumosum*, *Amblystegium scorpioides*, *A. falcatum*, *A. exannulatum*, *A. glaucum*, *Fontinalis antipyretica*, *Jungermannia inflata*, *Nardia emarginata*, etc., are often richly covered with these minute forms.

A large number of the microscopic unicellular and colonial Algae and Flagellata occur, along with an abundance of Copepoda and Rotifers, scattered through the surface layers of lakes, rivers, and other bodies of freshwater, and constitute the so-called *plankton* (see the frontispiece). Many of these organisms are sufficiently big not to pass through the meshes of the ordinary tow-nets used for plankton-work (cf. p. 13), and most of the accounts dealing with freshwater plankton have alone taken cognisance of such forms. In recent years, however, it has become known that there are innumerable plankton-organisms, some of very minute dimensions, which, either in their entirety or in great part, pass through the meshes of a tow-net and can only be obtained by centrifuging the water after it has drained through the net. The organisms constituting this *nannoplankton* are particularly Algae and Flagellata and as yet only relatively few of the more minute forms are known. It would appear however that in many cases they form a rather large percentage of the entire plankton.

The pigmented planktonic Protophyta of course constitute the chief source of food for the other plankton-organisms, mainly Rotifers and Crustacea. The animal and vegetable members of the plankton, moreover, furnish the food of most of the smaller aquatic animals and so, indirectly, form the basis of the food-material of lacustrine and river fishes. As yet few data are available concerning the food-value of the freshwater plankton and for many reasons it is not easy to arrive at a reliable estimate. Birge and Juday[3] have, however, investigated the matter comprehensively for some of the inland lakes of Wisconsin. They

[1] Chodat, Bull. Herb. Boissier, VI, 1898, p. 434.

[2] Weber van Bosse, Naturk. Verh. Holl. Maatsch. d. Wet., Ser. 3., V, 1887, p. 10.

[3] Wisconsin Geol. and Nat. Hist. Survey, Bull. No. 64, Scient. Ser. No. 13, 1922; see esp. p. 150.

estimate the mean quantity of dry organic matter in the standing crop of total plankton of Lake Mendota as amounting approximately to an average of 240 kilograms per hectare of surface (214 lbs. per acre). Given a monthly turnover in this mean quantity, there would be an annual production of 2800 kilograms per hectare (2568 lbs. per acre). Brandt[1] states that the chemical composition of the plankton of the Baltic Sea in autumn and winter is intermediate between that of "rich pasturage" and green lupines, the proportion of fat being greater than in land products used as fodder.

Many of the Algae found in the plankton are more or less characteristic of this habitat, some of them being largely and others entirely surface organisms[2]. The majority belong to the Volvocales, Chlorococcales, Desmidiaceae, Bacillariales, Chrysomonadales, Dinoflagellata, and Chroococcales. Many of the organisms concerned are provided with special flotation mechanisms, usually in the form of some kind of surface-enlargement. In many cases (especially among Desmids and Chlorococcales) these take the form of long spines (see fig. 34) or processes which terminate in spines (cf. also p. 100). In those species of Desmids which normally possess long spines, the latter are of greater length when the plants occur in the plankton than when found in other situations. It is possible that this spined condition is also to be correlated with the need for greater protection against those animals of the plankton which feed on Algae[3].

One or more plankton-Algae may sometimes develop in such abundance as to give a very definite coloration to the piece of water in which they occur. Such "water-bloom" is most commonly due to members of the class Myxophyceae, but many other forms may at times produce the same effect[4]. The presence of Algae in water, even in relatively small quantities, may give it a definite odour or taste; drinking water is sometimes rendered unfit for use owing to the presence of Myxophyceae, Diatoms, etc.[5] The majority of freshwater Algae, however, probably tend rather towards the purification than otherwise of a piece of water owing to their capacity to absorb and utilise many diverse kinds of organic substances.

[1] Wiss. Meeresunters. Abt. Kiel, III, 1898, p. 87; see also Amer. Naturalist, XXXII, 1898, p. 952.

[2] cf. especially West and West, 1909 *a*; Pearsall, Journ. Linn. Soc., Bot. XLVII, 1925, p. 55. No attempt is made here to deal even superficially with the enormous literature relating to freshwater plankton.

[3] W. and G. S. West, Journ. Linn. Soc., Bot. XXXV, 1903, p. 554.

[4] Naumann, Archiv f. Hydrobiol. u. Planktonk. XIII, 1922, p. 647; Smith, Roosevelt Wild Life Bull. II, 1924, p. 100.

[5] cf. Moore, Yearbook U.S. Depart. Agric. 1902, p. 175.

Many authorities[1] have drawn a distinction between *benthos*, the free or attached Algae of the littoral zone of a piece of water, and the plankton, comprising those forms which occupy the open water and are free-floating throughout their active vegetative existence. In large bodies of water, such as lakes, this distinction is not difficult to maintain, but in ponds and pools the plankton often comprises a mixture of true planktonic and benthic forms which has been styled *heleoplankton*. The latter has been investigated in great detail by Griffiths[2] who shows that the quality of the plankton depends largely on the depth at which sediments are situated and the consequent nature of their fermentation products, whether aerobic or anaerobic[3]. The plankton of rivers (*potamoplankton*) is largely derived from the backwaters and is often rich in Diatoms[4].

Algae can exist under very varied temperature-conditions. In temperate and arctic climates many of them can survive prolonged freezing, even when in the ordinary vegetative condition. It is quite possible to melt out from the ice numerous healthy Algae, which have suffered in no way from their exposure to such a low temperature. In the arctic and antarctic regions, in the Alps, and in the Andes, there exist snow-floras, consisting principally of Algae which pass their entire existence on the snow and ice. The members of this community (known as the "cryoplankton") commonly contain a red pigment, and such "red snow" includes a few forms which are more or less universal in such situations[5].

Algae also occur in warm streams, and the vegetation of hot springs consists exclusively of these organisms[6]. It has been affirmed that they can exist in hot water and hot vapour up to a temperature of 94·5° C. (200° F.)[7], but it may be doubted

[1] cf. West, 1916 *a*, p. 431.

[2] Griffiths, 1923; Griffiths, Journ. Linn. Soc., Bot. XLVII, 1925, p. 75.

[3] cf. also Pearsall, Rev. algol. I, 1924, p. 53.

[4] Fritsch, Ann. of Bot. XVII, 1903, p. 631; Butcher, Naturalist, 1924, p. 175.

[5] See especially Wittrock, Bot. Centralbl. XIV, 1883, p. 158; Lagerheim, Ber. Deutsch. Bot. Ges. X, 1892, p. 517; Chodat, Bull. Herb. Boissier, IV, 1896, p. 879, and Chodat, 1922, p. 75. The most interesting of these organisms are *Chlamydomonas nivalis* (Sommerf.) Wille and a Desmid, *Ancylonema Nordenskiöldii* Berggr. Sometimes snow-floras exhibit other colours than red; "yellow snow" is evidently of frequent occurrence in the antarctic (Fritsch, Journ. Linn. Soc., Bot. XL, 1912, p. 297) and has also been recorded in the Alps.

[6] cf. Cohn, Abhandl. Schles. Ges. f. vaterl. Kultur, 1862, p. 35; Weed, Amer. Naturalist, XXIII, 1889, p. 394; Bohlin, Bih. Sv. Vet.-Ak. Handl. XXVII, Afd. 3, No. 4, p. 12; West, Journ. of Bot. XL, 1902, p. 241.

[7] Brewer, Amer. Journ. Sci., ser. 2, XLI, 1866, p. 391.

whether such statements would stand a critical investigation. Some of these forms become encrusted with carbonate of lime or with silica and play no small part in the formation of the deposits which are generally found in the neighbourhood of hot springs (cf. p. 450). It is worthy of note that the Algae which occur at very high altitudes and which therefore exist at relatively low temperatures, and those which inhabit the hottest springs are, with few exceptions, species of Myxophyceae and Bacillariales[1].

Various investigators[2] have conducted experiments with a view to ascertaining how far freshwater Algae can withstand exposure to salt water. Comère found that forms with a robust structure and large chloroplasts can best survive such treatment; some species of *Oedogonium* and *Cladophora* could live in a 3·5 per cent. solution of sodium chloride, and some of the larger species of *Spirogyra* in solutions of 1·8–2 per cent. In all cases the salinity of the water caused an increase in cell-size and, when the concentration was high, malformation of the cells invariably occurred. Many terrestrial Algae seem able to withstand prolonged exposure to saline solutions. In all these cases however there is little or no growth. Relatively few Algae can exist near the mouths of rivers, where there is a frequent change in the salinity of the water; the successful forms (*Enteromorpha*, *Bangia*, *Fucus ceranoides*, etc.) are partly marine and partly freshwater.

No inconsiderable number of Algae are able to thrive in terrestrial situations[3], and many of these are often important as pioneers in the colonisation of exposed rock-surfaces[4] and other substrata. In recent years various researches have shown the existence of a well-marked subterranean soil-flora[5], comprising Green and Blue-green Algae, as well as Diatoms. The majority of the terrestrial Algae are distinct from the aquatic ones and those occurring in the more exposed habitats (soil-surface, tree-trunks, etc.) are often highly adapted to resist prolonged exposure to drought without any appreciable change from the normal vegetative condition[6]. This capacity is also displayed

[1] The same is true of the algal flora within the antarctic circle.

[2] Richter, Flora, LXXV, 1892, p. 4; Comère, Nuova Notarisia, XIV, 1903, p. 18, and Bull. Soc. Bot. France, LII, 1905, p. 226; Fritsch and Haines, Ann. of Bot. XXXVII, 1923, p. 706.

[3] Fritsch, Journ. of Ecol. X, 1922, p. 220.

[4] Fritsch, Geogr. Journ. 1907, p. 531; Fritsch and Salisbury, New Phytol. XIV, 1915, p. 129.

[5] Esmarch, Hedwigia, LV, 1914, p. 224; Petersen, Mem. Acad. Roy. Danemark, 7 sér. XII, 1915, No. 7; Bristol, 1920.

[6] Fritsch, 1922; cf. also Ann. of Bot. XXX, 1916, p. 135.

by the resting-stages of aquatic Algae, whose vegetative phases are usually very susceptible to the absence of moisture.

Few Algae are to be found in equal amount all the year round. In fact many exhibit more or less restricted periods of abundance and between such periods, which often occur but once a year, they are either completely absent (their resting-stages being buried in the mud) or are only represented in very diminished numbers. As a result, especially in more or less standing waters, there is generally a very pronounced periodical succession of the Algae, one phase following upon the other, and similar phases occurring at approximately the same times in successive years. This periodicity is very well marked in the case of the plankton[1], but is also quite patent in many of the larger filamentous Algae of ponds and lakes. A careful study of the times of maximum abundance of such forms in successive years[2] has already shed much light on the conditions determining the development of different Algae, and it is much to be desired that such work should be further prosecuted. It is not known as yet whether such periodicity is exhibited by the terrestrial algal flora.

The comparative richness of any district in freshwater Algae depends very largely on its physical geography and on the geological formation. Mountainous tracts are more prolific than flat districts, even though many of the larger Algae are absent from them. Most of the filamentous and an abundance of the commoner unicellular forms are found in low-lying quiet waters. In mountainous areas filamentous Algae are chiefly represented by the Myxophyceae (Cyanophyceae) and Conjugatae, the presence of numerous species of *Mougeotia* being a marked feature of such districts, while the unicellular forms are greatly increased by the occurrence of numerous Desmids. If the mountains consist of the older Palaeozoic rocks, of Pre-Cambrian rocks, or of rocks of igneous origin, there is a surprising numerical increase, not merely of species but also of individuals; and in comparison, a mountainous district of carboniferous limestone or other calcareous formation is distinctly poor.

Thus, the English Lake District, Wales, and certain parts of Scotland and Ireland (especially the small tarns and peat-bogs which lie in the hollows of the Lewisian gneiss of north-west

[1] cf. e.g. West and West, 1912.

[2] Fritsch, New Phytol. v, 1906, p. 149; Fritsch and Rich, Ann. of Bot. xxi, 1907, p. 423; Fritsch and Rich, 1909 and 1913; West, New Phytol. viii, 1909, p. 181; Hodgetts, 1921; Pearsall, Journ. of Ecol. xi, 1923, p. 165. The bulk of the foreign literature merely establishes the fact of periodicity; see however Comère, Bull. Soc. Bot. France, liii, 1906, p. 390, and Transeau, Trans. Amer. Microscop. Soc. xxxii, 1913, p. 31.

Scotland) yield a much greater variety of Algae than any other parts of the British Isles. The plankton of the larger lakes in these areas is also often much richer in Desmidiaceae than any that has been described elsewhere. W. and G. S. West[1] showed that the rich Desmid-floras of these regions occur where there is an abundant rainfall and a drainage-water derived from geological formations older than the Carboniferous. Subsequently Pearsall[2] related the occurrence of a Desmid-plankton in certain lakes of the Lake District to the stage of evolution of the lake-basin, the rocky (primitive) lakes being those with a plankton dominated by Desmids. This he ascribes to the high ratio of sodium-potassium to calcium-magnesium in the latter type of lake[3]. The poorest area of all for British freshwater Algae is the fen district in the east of England[4].

Most unicellular Algae and some of the filamentous ones, unless specially protected as in many Desmids, are readily taken as food by Amoebae, Turbellarians, Oligochaetes, Tardigrades, and Crustacea (cf. also p. 5). Tadpoles feed almost exclusively on the larger filamentous Algae and many freshwater fish derive a smaller or larger part of their nourishment from the same source[5]. A considerable proportion of the food of freshwater Lamellibranchs also consists of living and decaying Algae.

The subjoined list indicates the kinds of Algae and Flagellata that are commonly to be encountered in a number of different habitats[6]. The list must not be regarded as in any way complete, since only the more characteristic forms are mentioned. Species are only given, when they are practically restricted to the habitat in question or are exceedingly distinctive of it.

Ponds[7] *and ditches.* Chlamydomonas, Gonium pectorale, Pandorina morum, Eudorina elegans, Volvox, Glococystis gigas, Tetraspora, Micractinium, Oocystis, Nephrocytium Agardhianum, Ankistrodesmus, Dictyosphaerium Ehrenbergianum, Westella botryoides, Scene-

[1] West and West, 1909 *a*, p. 195 et seq.

[2] Proc. Roy. Soc. B, xcii, 1921, p. 276 et seq.

[3] cf. also Pearsall, Rev. Algol. 1, 1924, p. 53.

[4] West, 1899, p. 49.

[5] cf. for example Comère, Mem. Acad. Sci. Toulouse, 11 sér. v, 1917, p. 409. G. S. West (1904, p. 7) mentions that an examination of the intestine of *Ceratodus*, the Australian mud-fish, revealed "masses of sticks, twigs, leaves, fragments of Hepatics, etc., all of which would have been taken in by the fish from the muddy bottom of the water in which it lived. This material would be mostly in a dead condition before being swallowed; but a microscopical examination shows amongst it the decomposed remains of many kinds of Algae, including thousands of the empty valves of Diatoms."

[6] cf. also West, 1916 *a*, p. 418 et seq.

[7] With reference to the plankton of ponds and pools, see Griffiths, 1923; and Griffiths, Journ. Linn. Soc., Bot. xlvii, 1925, p. 75.

desmus, Coelastrum, Pediastrum, Ulothrix subtilis var. variabilis, Enteromorpha intestinalis (also canals), Microspora, Rhizoclonium hieroglyphicum, Cladophora fracta (only when well aerated), Chaetophora incrassata, Microthamnion Kützingianum (favours peat), Gongrosira, Oedogonium, Spirogyra, various Desmids (not usually abundant), Vaucheria; Botryococcus Braunii, Ophiocytium, Tribonema bombycinum (shaded pools or such as are grass-grown at the margin); Synerypta Volvox, Synura Uvella; Melosira varians, Meridion circulare, Asterionella formosa, Amphiprora paludosa, Nitzschia acicularis, and many other less characteristic Diatoms; Cryptomonas; Peridinium cinctum, Ceratium cornutum; various Euglenineae (especially if water rich in organic matter); Merismopedia, Gomphosphaeria aponina, Nostoc, Tolypothrix, Scytonema crispum, Gloeotrichia, and many Oscillatoriaceae.

Rain-pools. Chlamydomonadaceae, Sphaerella lacustris; Synura Uvella; Euglenineae.

Lakes. The benthic flora is exceedingly varied, but has few characteristic forms (Oedogoniaceae, Chaetophora, Microspora, Cladophoraceae, Mougeotia; Tabellaria). Typical constituents of the plankton are: Sphaerocystis Schroeteri, Pediastrum, Quadrigula Pfitzeri, Oocystis, Kirchneriella, Dictyosphaerium Ehrenbergianum, Westella botryoides, Coelastrum, Staurastrum, and other Desmids; Botryococcus Braunii; Mallomonas, Dinobryon; Cyclotella, Rhizosolenia, Tabellaria, Fragilaria, Synedra, Asterionella, Surirella, and other Diatoms; Peridinium (esp. P. inconspicuum), Ceratium (esp. C. Hirundinella); Coelosphaerium, Gomphosphaeria, Microcystis, Anabaena, Lyngbya (often spirally coiled).

Mountain tarns and lakes. Binuclearia tatrana, Mougeotia; Tetracyclus lacustris.

Rivers, cataracts, and other types of flowing waters. Ulothrix zonata, Hormidium rivulare, Microspora amoena, Chaetomorpha Linum, Cladophora glomerata, Stigeoclonium (slow-flowing waters and springs), Draparnaldia (slow-flowing), Chaetophora pisiformis, Sirogonium sticticum (slow-flowing); Melosira, Gomphonema geminatum; Chantransia, Batrachospermum (slow-flowing), Lemanea, Hildenbrandtia rivularis; Xenococcus britannica, Phormidium (esp. P. Retzii), Nostoc.

Bogs and boggy pools. Schizochlamys delicatula, Eremosphaeria viridis, Oocystis solitaria, Chaetosphaeridium globosum, Geminella mutabilis, Draparnaldia, Chaetophora, Spirotaenia, Cylindrocystis Brebissonii, Netrium Digitus, Penium polymorphum (upland moorlands), Closterium gracile and many other sp. of Closterium, Euastrum, Micrasterias, Cosmarium (esp. C. Cucurbita), Staurastrum margaritaceum (upland moorlands), Xanthidium armatum, Gymnozyga moniliformis, and a great diversity of other Desmids, Zygnema anomalum; Botryococcus Braunii, Chlorobotrys regularis; Melosira granulata, Stauroneis Phoenicenteron, Navicula rhomboides var. saxonica; Glenodinium uliginosum; Batrachospermum; Gloeothece,

Aphanothece, Microcystis, Chroococcus turgidus, Hapalosiphon, Stigonema ocellatum, Glaucocystis Nostochinearum.

Brackish pools. Brachiomonas, Dunaliella, Enteromorpha intestinalis; Spirulina tenuissima, Lyngbya aestuarii.

Salt-marshes. Rhizoclonium; Chroococcus turgidus, Microcoleus Chthonoplastes, Lyngbya aestuarii.

Wet rocks (often amid Mosses and Liverworts). Mesotaenium, Cylindrocystis crassa, Cosmarium (esp. C. Holmiense, C. anceps); Melosira arenaria, M. Roeseana, Denticula, Gomphonema geminatum, Cymbella cuspidata (last two esp. in upland districts), Navicula borealis; Gloeothece, Aphanothece, Gloeocapsa, Aphanocapsa, Phormidium, Schizothrix, Nostoc, Scytonema Myochrous, S. mirabile, Stigonema.

Damp ground (surface). Palmella miniata, Hormidium flaccidum, Stichococcus bacillaris, Prasiola, Mesotaenium, Cylindrocystis crassa, Zygogonium ericetorum (esp. heaths), Vaucheria; Botrydium (damp mud); Hantzschia amphioxys; Porphyridium cruentum; Phormidium (esp. P. autumnale), Symploca muralis, Microcoleus vaginatus, Nostoc commune, Cylindrospermum majus.

Subterranean soil-flora[1]. Chlorococcum humicolum, Trochiscia aspera, Ulothrix subtilis var. variabilis; Bumilleria exilis; Navicula (esp. N. mutica, N. atomus), Hantzschia amphioxys; Plectonema Battersii, Phormidium; and Moss-protonema.

Tree-trunks, palings, etc.[2] Chlorococcum humicolum, Trebouxia, Stichococcus bacillaris, Trentepohlia, Pleurococcus; Symploca muralis.

The commonest epiphytes. Characium, Protoderma viride, Aphanochaete, Coleochaete, Chaetopeltis orbicularis, Bulbochaete; Characiopsis, Ophiocytium Arbuscula; Synedra splendens, Achnanthes, Cocconeis, Rhoicosphenia curvata, Gomphonema, Cymbella, Epithemia; Chamaesiphon.

The Collection, Preservation, and Investigation of Freshwater Algae

For the collection of freshwater Algae a plentiful supply of small wide-mouthed tubes or bottles will be found most useful. Only small quantities of the larger, strictly aquatic Algae should be put into a tube together with plenty of water, and the tube should not be more than three-quarters full. This is because rapid decomposition accompanies overcrowding, and it may frequently happen that collections cannot be examined for many hours after they have been made. Most microscope-makers however manufacture small portable microscopes with the help of which an immediate examination of living material can be made at the time of collection.

[1] See especially Bristol, 1920.

[2] cf. also Brand, 1925.

To gather the minute Algae that occur attached to larger water plants, the latter should be removed from the water with as little mud as possible and the superfluous moisture allowed to drain away for a few minutes. They should then be gently squeezed over a wide-mouthed bottle and the issuing water collected in the latter. In the sediment which settles at the bottom will be found numerous unicellular and colonial Algae[1]. Sometimes one or two hundred species may be obtained from a small quantity of such material.

The Algae of the *plankton* are collected by means of tow-nets having the shape of elongated cones with truncated apices, varying in length from one to two feet, and composed of the finest bolting silk[2]. There are many different types, but unless quantitative work is to be undertaken a simple form will suffice. According as only the surface plankton (generally the richest in Algae) or that of deeper layers is required, the net must be towed horizontally or vertically, in the latter case from a stationary boat. For the collection of *nannoplankton* two methods are in use[3]. Where such plankton is rich, it is often sufficient to centrifugalise a small quantity of the water; in other cases it is advisable to pump up a certain amount of water and filter it through filters made of hardened paper. A consideration of the numberless other appurtenances connected with plankton-investigation is beyond the scope of this book[4].

If algal material is to be kept living for some time, it is best placed in wide-mouthed jars with an abundance of water, and not exposed to too strong a light. Sterile species of Zygnemaceae and Oedogoniaceae will often become fertile under these conditions. Some filamentous Algae also keep well, if placed in flat glass dishes with a small amount of water[5].

Whenever possible, Algae should first be examined in the living state, as many characteristics tend to be lost or obscured in preserved material, and many of the Flagellates (e.g. species of *Euglena*) can only be determined when alive. On the other hand, many species of Desmids and Diatoms, especially those with characteristic surface-markings, cannot be identified with certainty unless dead empty cells are available.

[1] If the material be mixed with a considerable amount of mud, a centrifuge will be found useful to separate out the Algae.

[2] cf. Sutherland, Journ. Ecol. I, 1913, p. 166; Juday, Trans. Wisconsin Acad. Sci. XVIII, 1916, p. 566; also West and West, 1909 *a*, p. 166.

[3] See especially Bachmann, Biol. Centralbl. XX, 1900, p. 386; Lohmann, Int. Rev. Hydrobiol. u. Hydrogr. IV, 1911, p. 1; Scourfield, Journ. Quekett Micr. Club, XI, 1912, p. 243.

[4] cf. Ward and Whipple, Freshwater Biology. New York, 1918, p. 67 et seq.

[5] For the cultivation of Algae, see p. 16.

For the observation of cilia of motile forms a 1–2 per cent. cocaine solution is very useful; iodine or dilute acid fuchsin in aqueous solution often brings them out more clearly. Rapid fixing by inverting a slide or cover-glass bearing a drop of material for a few minutes over 1 per cent. osmic acid usually achieves the same object[1]. Inconspicuous mucilage-envelopes are best seen by adding sepia or Indian ink to the water containing the material; they can also be stained with methylene blue or methyl violet in aqueous solution[2].

In preserving Algae for future examination, the fluid used will depend on the nature of the material and the purpose for which it is ultimately required. The grosser features of cell-structure, such as usually suffice for specific determination, are well preserved in many forms by a 2–4 per cent. solution of formalin (= 40 per cent. formaldehyde); such material is also usually in good condition for subsequent staining. Formalin is almost equalled by a dilute solution of picric acid, but this is not suitable for plankton. If only the cell-outlines and the structure of the cell-wall are required, there is no better preservative than a 4 per cent. solution of potassium acetate (containing a trace of copper acetate). An equal volume of this solution added to the water in which the Algae are living is quite sufficient. The most difficult of the pigmented Protophyta to preserve are the Chrysomonadales, since most preservatives cause complete disorganisation; pure formalin has been advocated as giving fairly satisfactory results.

If the finer features of cell-structure are to be studied, more careful fixation is required. The method to be employed will vary with the kind of material and the stains to be used subsequently and for each individual case can only be determined by comparison. No purpose would be served by an enumeration of the numerous fixatives in use[3]. Among the more serviceable may be mentioned chrom-acetic (70 c.c. 1 per cent. chromic acid, 5 c.c. glacial acetic, 90 c.c. water), Bouin's picro-formol-acetic (concentr. picric acid 15 c.c., 30 per cent. formalin 5 c.c., glacial acetic acid, 1 c.c.), and hot corrosive sublimate (3 grm., with glacial acetic 3 c.c., 50 per cent. alcohol 100 c.c.), the last used especially by Carter[4] in studying the chloroplasts of Desmids. Small forms, previously preserved in formalin, may be allowed

[1] cf. also Deflandre, Bull. Soc. Bot. France, LXX, 1923, p. 738.

[2] See also Schröder, Verh. Nat.-med. Ver. Heidelberg, VII, 1902, p. 141.

[3] cf. especially as regards fixation and staining: v. Wellheim, Jahrb. Wiss. Bot. XXVI, 1894, p. 674; Chamberlain, Methods in Plant Histology, Chicago, 1924, p. 173 et seq.; Lemmermann, 1910, p. (12) et seq.; Smith, Plant World, XVI, 1913, p. 219.

[4] Ann. of Bot. XXXIII, 1919, p. 218.

to dry on the slide, washed in water overnight, and then stained *in situ*. This often affords good results. The stains used will depend on the material and the structure to be studied; one of the most useful is Heidenhain's iron-alum-haematoxylin[1]. Geitler[2] advocates treatment of the living Algae with a boiling 5–10 per cent. silver nitrate solution for a short time (30 secs. to 5 mins.) as a method of fixing the cell-contents and at the same time bringing out the chloroplasts which take on a brown to black coloration.

Some of the coarser Algae can be preserved by drying, either on paper or on slips of mica, but a fluid preservative is nearly always more suitable. The Myxophyceae alone give moderately good results, since on soaking out again in water they regain much of their original freshness and are usually found to have retained their bright colours. In examining exsiccata addition of a drop of concentrated lactic acid to the water in which the material is being soaked often affords very good results.

Algae are best mounted in the fluid in which they have been preserved and the preparations may be sealed with gold-size or marine glue dissolved in xylol. Everyone who has had any experience of fluid mounts, however, knows quite well that if the specimens keep for a long time it is due more to good fortune than to any other cause. Even the best fluid mounts frequently begin to dry up after some time by the formation of air-bubbles in the centre of the slide which gradually extend towards the periphery. The only explanation of this is the porous nature of the thin cover-slip. Material can also be mounted in dilute glycerine which is then allowed gradually to concentrate before putting on the cover-glass[3]; the preparation can be sealed as described above. Such mounts are rather more permanent, but the material is liable to be distorted and, unless previously stained, to become too transparent. These objections apply still more forcibly to the use of glycerine gelatine. Material that has been stained for cytological investigation is generally mounted in Canada balsam according to the usual methods (cf. Chamberlain, loc. cit.).

For the investigation of Diatoms a somewhat different procedure is adopted[4]. Since specific, and even generic, determination is as a rule based entirely on the structure and marking of the

[1] With reference to *intra vitam* staining of Algae, see especially Brand, 1925, p. 290 et seq. A solution of methyl green in 1 per cent. acetic acid will often bring out nuclei.

[2] Österr. Bot. Zeitschr. LXXI, 1922, p. 116.

[3] See Evens, Journ. Quekett Microscop. Club, XIV, 1922, p. 225.

[4] cf. Smith, Synops. Brit. Diat. I, 1853, p. XXX; Meister, Kieselalg. d. Schweiz, 1912, p. 11 et seq.

siliceous membrane, it is necessary to get rid of all but the latter. This is most simply accomplished by boiling material containing Diatoms in concentrated nitric or sulphuric acids; in the latter case small amounts of potassium nitrate are afterwards carefully added until the dark colour disappears. The resulting liquid is diluted with a considerable bulk of water, shaken up, and allowed to sediment; the clear liquid is poured off, fresh water added, the whole once again shaken, and this is repeated until the water no longer shows any trace of an acid reaction. For the more delicate forms less violent methods are appropriate (cf. Lemmermann, 1910, p. (12)). A small drop of the sediment is then allowed to dry on a slide or cover-glass and mounted in Canada balsam, dammar, or styrax; the last-named is especially suitable for the detection of the finest markings of the Diatom-valve. It is necessary to use very thin cover-glasses (No. 1), since for the investigation of the smaller species oil-immersion lenses have to be employed.

In examining Algae, in following out their life-history, and in identifying them, they should always be carefully drawn to scale with the help of a camera lucida. This is the surest means, after determining the magnification, of obtaining accurate measurements[1] and also the best way of impressing their diagnostic features on the memory. Great attention should be paid by all students of Algae to the characters of the cells, the structure of the cell-wall, the form and arrangement of the chromatophores, the presence or absence of pyrenoids, etc. No one can acquire erroneous ideas of such common genera as *Ulothrix*, *Microspora*, *Tribonema*, and others, if he has once realised their distinctive cell-features. It should however be understood that many Algae at times assume forms (e.g. the so-called *Palmella*-stages) that render their recognition difficult or impossible, so that a determination is only feasible if further material can be obtained from the same habitat at a later date. Especially in looking over a preserved sample, there is often much that is best left undetermined.

The Cultivation of Algae

In the investigation of the life-histories of Algae it is often desirable to cultivate them. This is most simply done by placing some of the algal material in a suitable nutrient solution, composed of pure mineral salts dissolved in glass distilled water, although sometimes good results are obtained in pure water.

[1] The dimensions of an Alga can also be determined directly with the help of a micrometer eye-piece, the result being expressed in terms of μ (thousandth of a millimetre).

A number of such solutions have been employed by different investigators with considerable success[1]. The cultures must be kept at a suitable temperature, which will vary with different types of Algae, although 20° C. is a good average temperature; the intensity of the illumination must also be controlled. Even under such circumstances, however, it must always be borne in mind that the conditions are not likely to be identical with those obtaining in the natural habitat of the plants, and strange forms may be developed which need not necessarily belong to the normal life-cycle. As far as possible such methods should always be supplemented by frequent study of the Alga in a state of nature. Where direct observation for a brief period is desirable, hanging-drop cultures often afford satisfactory results; conditions, however, readily become abnormal in such cultures after a little time.

The majority of Algae occur in impure gatherings, in which one form is intermingled with a large number of others, partly Algae and Flagellata, partly other organisms (Bacteria, Fungi, etc.); it is only very exceptionally that one finds a practically pure growth consisting almost entirely of one algal form. In order to be able to study accurately the life-history of an Alga, however, it is frequently essential to have it in *pure culture*[2]; this is especially true of the simpler unicellular and colonial forms, and during the last 25 years much work has been done with such pure cultures. It is not difficult by one method or another to obtain a pure culture containing only one form of Alga[3], but it is much more difficult to obtain such cultures free from admixture of Bacteria.

Pure cultures of the larger Algae can often be obtained by transferring a single filament to a suitable sterilised nutrient medium with the help of a sterilised needle[4]. In the case of

[1] Klebs (1896, p. 8) used Knop's nutritive solution, containing four parts calcium nitrate and one part of each of magnesium sulphate, potassium nitrate, potassium phosphate; the three last are first dissolved in pure water and then the solution of the calcium nitrate is added, the whole being diluted to a strength varying between 0·2 and 0·5 per cent. Bristol (1920, p. 37) used a culture-solution having the following composition: 1 grm. potassium dihydrogen phosphate, 1 grm. sodium nitrate, 0·3 grm. magnesium sulphate, 0·1 grm. calcium chloride, 0·1 grm. sodium chloride, a trace of iron chloride, 1000 c.c. distilled water.

[2] cf. Klebs, 1896, p. 175 et seq.

[3] Beijerinck, Bot. Zeit. XLVIII, 1890, p. 725; Klebs, 1896, p. 184; Chodat et Grintzesco, Comptes Rendus Congr. internat. Bot. Paris, 1900, p. 157; Grintzesco, Bull. Herb. Boissier, sér. 2, v, 1902, p. 225; Richter, Ber. Deutsch. Bot. Ges. XXI, 1903, p. 493 (Diatoms); Wettstein, Österr. Bot. Zeitschr. LXX, 1921, p. 23.

[4] Full precautions must naturally be taken to ensure that all vessels, etc., used in these operations are completely sterilised according to the recognised methods.

unicellular and colonial forms a small quantity of the material should be shaken up with a relatively large bulk of water and a drop of this transferred to the culture medium; if this does not give a pure growth, the same operation may be repeated with a small portion of the culture. It may often be necessary to carry out this procedure again and again. The most satisfactory way of obtaining a pure culture is to start with a single individual. To accomplish this in the case of the smaller forms, however, requires much patience. The method depends on sucking up a single specimen with the help of a sterilised pipette from a small quantity of material placed in a watch-glass and observed under the low power of the microscope.

Many workers with pure cultures have grown the Algae on gelatine or agar-agar and it is remarkable how large a number of diverse algal forms will thrive on such substrata; the growth is in the main confined to the surface of the medium. The remarks made above about the possible occurrence of unnatural conditions in algal cultures, however, apply even more strongly to such as are grown on solid media. Cultures of this kind have been of value in elucidating features of the life-histories of many forms[1], but much that has been gleaned from them is of doubtful value from the point of view of a knowledge of the natural life of the lower organisms. Cultures on damp porcelain plates have also been tried with success.

A direct investigation of the subterranean soil-flora is practically impossible and cultures, in which the dried soil is added to a suitable nutrient medium, afford the only means of determining the algal organisms present[2]. A modification of this method in which diverse organic substances are added to water containing the soil often leads to an exceptional development of one or a few forms[3].

The Classification of the Pigmented Protophyta (Flagellata and Algae)

It will be a familiar fact that, apart from the very frequent occurrence of motile reproductive cells (zoospores, gametes) in the life-cycles of many Algae, there exist a large number of forms—many of them unicells (e.g. *Chlamydomonas*, cf. also fig. 1)—in which the ordinary individuals exhibit active movement throughout their vegetative existence. While the motile reproductive cells are invariably naked (save the gametes of a few species of Chlamydomonadaceae, see p. 62), the independent free-moving unicellular and colonial types are either naked or

[1] cf. e.g. Chodat, 1913.
[2] cf. Bristol, 1920, p. 37.
[3] cf. Jacobsen, Zeitschr. f. Bot. II, 1910, p. 147.

provided with a definite cell-membrane similar to that of other plants. Organisms possessing such a cell-wall, in so far as their cells were provided with chromatophores, have been classed among the Algae, whilst the naked forms have been referred to the Flagellata. The latter were also characterised by reproduction being effected by fission in the longitudinal plane, by the almost invariable absence of sexual reproduction, and by a ready capacity for cyst-formation. Included in the Flagellata are numerous colourless types[1], some of which appear to be very closely related to the pigmented forms and may have originated from them secondarily. The flagellate characteristics just mentioned are not however purely confined to motile or unicellular types, since a large number of forms are known which, while showing these features, are sedentary throughout a great part of their life or exhibit a multicellular habit.

A review of the different types of Algae and Flagellata shows that altogether analogous forms may in one class exhibit algal characteristics (possession of a cell-wall, sexuality, etc.) and in another flagellate characteristics (cf. supra). Thus, the majority of the motile unicells among the Isokontae are Algae, the equivalent forms among Heterokontae and Chrysophyceae are Flagellates, and the same fact emerges if one compares other types of construction found in the different classes. It is therefore probably unwise to stress too much the differences between algal and flagellate organisation. The algal characteristic of possessing a definite cell-wall is one which probably appeared at different stages in the evolution of the various classes of Protophyta, and we shall certainly not go far wrong if, for instance, we regard the bulk of the Chlamydomonadales as scarcely less primitive by comparison than the Chrysomonadales. True the latter lack sexuality, but that also is a feature that has not necessarily originated in every phylum of Protophyta (cf. Myxophyceae). Nor is the method of longitudinal division purely a characteristic of the Flagellates. For these various reasons it no longer appears logical to separate sharply Algae and Flagellata (altogether an impossibility in the class Heterokontae), the more so as much that is especially instructive from the standpoint of comparative evolution is altogether lost sight of when that is done.

There are probably few who would doubt nowadays that an early phase in the evolution of the simpler pigmented Proto-

[1] Many of these are saprophytes, whilst others exhibit holozoic nutrition (i.e. ingestion of solid food), which is occasionally also met with in the pigmented types and even in true Algae (cf. Pascher, Ber. Deutsch. Bot. Ges. XXXIII, 1915, p. 427).

phyta was in all cases a unicellular uninucleate organism provided with special photosynthetic pigments lodged in more or less sharply differentiated parts of the cytoplasm, the *chromatophores*, and sooner or later acquiring special propelling organs in the shape of complex prolongations of the cytoplasm, the *flagella* or *cilia*. We may expect to find in the free-moving unicellular organisms of the present day a semblance of what these early forms of Protophyta were like. Moreover, we are justified in regarding the fundamental differences that they exhibit among one another as illustrative of diverse evolutionary trends that originated during the early beginnings of life, how and from what ancestry we know not. The classification of the innumerable types of motile unicells is still in its beginnings, the more so as new forms are constantly being discovered, but it is already clear that there are many different series. These are distinguished by the number and mode of arrangement of the cilia, the nature of the pigments contained in the chromatophores, the forms in which the products of photosynthesis are stored up in the cells, and by other less constant and therefore less important features[1].

Among the colonial and cellular (filamentous) Protophyta (both Algae and Flagellata) there are some which exhibit not only the same pigments in the chromatophores and the same photosynthetic products as are found in certain series of motile unicells, but their motile reproductive cells (swarmers) exhibit the same type of ciliation (compare for instance the zoospore of *Ulothrix* (fig. 3, D) or *Tetraspora* with the individuals of a *Chlamydomonas* (fig 1, A) or *Carteria* (fig. 5, A); or the swarmer of *Chrysosphaera* (fig. 2, G) with a *Chromulina* (fig. 1, C)). These resemblances were matters of frequent comment, but it was not until nearly the end of the last century (cf. p. 3) that the full conclusion was drawn from them and the doctrine of the origin of the Algae from motile unicellular forms clearly expounded. Every class of Protophyta was conceived as beginning with motile unicellular types of a distinctive kind. It thus became apparent, thanks to the work of Borzi, Luther, and Bohlin, that the class of the Green Algae (Chlorophyceae) included members of two totally distinct classes (Isokontae and Heterokontae) sharply distinguished from one another by the essential characteristics above mentioned (see also p. 295). In both these series more or less simple unicellular types and more elaborate multicellular "algal" forms were represented. There still remained however a number of series of motile unicells of which no higher "algal"

[1] cf. Süsswasserflora Deutschlands, Österreichs, u. der Schweiz, 1, 1914, p. 28.

members were known, and alternatively there were such large classes as the Phaeophyceae and Rhodophyceae of which no certain unicellular representatives had been discovered.

The second half of this statement still applies at the present day, but the researches of Klebs, Pascher, and others have shown that in a number of classes, until recently deemed purely "flagellate," forms with "algal" organisation also exist (e.g. Chrysophyceae, Dinophyceae), and it is possible that in the future all the old flagellate groups will be shown to comprise some algal representatives. Whether that happens to be the case or not, we are justified in giving them equal status with the groups in which evolution of such forms has occurred. As regards the algal groups in which no flagellate representatives are known, they afford sufficiently clear evidence of a separate ancestry, either in the possession of swarmers of a distinctive type (Phaeophyceae) or, where these are lacking, in the presence of special pigments and photosynthetic products (Rhodophyceae, Myxophyceae) or other peculiar features (Bacillariales).

On the basis of these considerations it is possible to distinguish the following 11 classes of pigmented Protophyta:

I. *Isokontae*[1], with chromatophores which are pure green and contain the same four pigments (two green, two yellow), and approximately in the same proportions, as in the higher plants. Starch is the customary form of storage of the products of photosynthesis, and pyrenoids are frequently present in the chromatophores. The algal members have a cell-wall in which cellulose is usually the main constituent. The motile cells (fig. 1, A) exhibit the same features and possess a number of equal cilia (commonly two or four) which arise from the front end of the swarmer and are all similarly orientated. In many members the cells contain one or few chromatophores. The majority of the representatives are "algal," many exhibit sexuality, and the class is much more widely represented in fresh than in salt water.

II. *Heterokontae*, with chromatophores which are yellow-green owing to the presence of an excess of the yellow xanthophyll. Starch and pyrenoids are absent, fat being the customary storage-product. The "algal" members have a cell-wall which is often rich in pectic compounds and which is frequently composed of two pieces overlapping at their edges. Resting stages with a silicified membrane are of common occurrence. The motile cells (fig. 1, B) possess two very unequal cilia (or sometimes only one?) arising from the front end. As a general

[1] With reference to the groups Stephanokontae and Akontae, see pp. 220 and 224.

rule the cells contain a number of discoid chromatophores. The majority of the members are "algal" and the class is more widely distributed in freshwater than in the sea. Sexual reproduction has only been observed in a few forms.

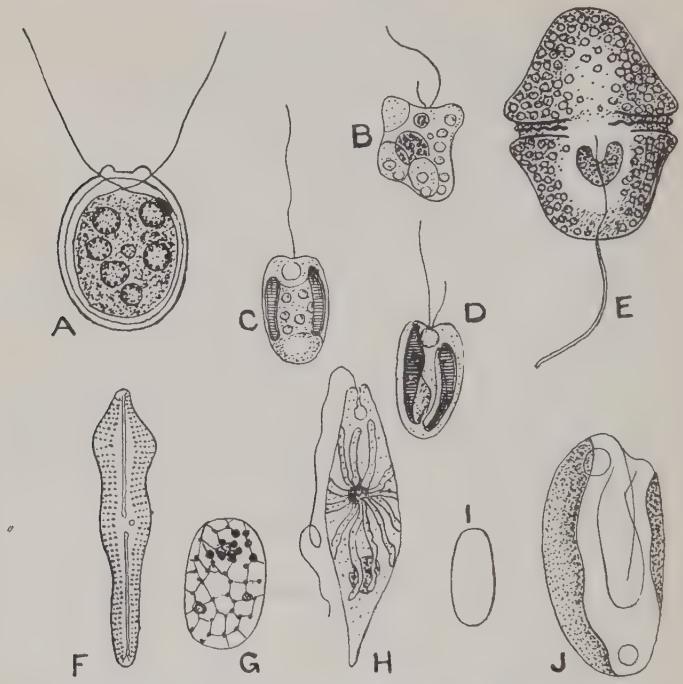

Fig. 1. Motile or other types of cell characteristic of the different classes of Protophyta. A, *Chlamydomonas sphagnicola* Fritsch & Takeda, from Keston, Kent (× 1000)—Isokontae. B, *Chloramoeba heteromorpha* Bohlin (after Bohlin)—Heterokontae. C, *Chromulina ovalis* Klebs (after Klebs, × 1500)—Chrysophyceae. D, *Ochromonas mutabilis* Klebs (after Pascher, × 600)—Chrysophyceae. E, *Glenodinium cinctum* Ehbg. (after Schilling)—Dinophyceae. F, *Gomphonema acuminatum* Ehbg. (after Meister, × 600)—Bacillariales. G, *Merismopedia elegans* A. Br., stained cell showing the simple structure (after Acton, × 2500)—Myxophyceae. H, *Euglena viridis* Ehbg. (after Lemmermann, × 550)—Euglenineae. J, *Cryptomonas ovata* Stein[1] (after Pascher, × 1200)—Cryptophyceae. I, optical section of *C. compressa* Pascher (× 1200).

III. *Chrysophyceae*, with brown or orange-coloured chromatophores containing one or more accessory pigments (phycochrysin). Starch and pyrenoids are absent, fat and leucosin being the customary forms of food-storage. The majority of the members are "flagellate" and are devoid of a special cell-membrane.

[1] The two cilia are not shown in the figure.

Many develop characteristic cysts arising endogenously and provided with an envelope composed of two, often very unequal, pieces (fig. 133, E, F) and frequently silicified. The motile cells (fig. 1, C, D) possess one or two cilia attached at the front end; in one series the cilia are unequal. The cells typically contain one or two laterally placed chromatophores. No sexual reproduction. The class is confined to freshwater.

IV. *Bacillariales* (*Diatomales*), with yellow- or golden-brown chromatophores containing, apart from the usual ones, an accessory brown pigment, diatomin. Bodies like pyrenoids often present; the products of photosynthesis are fat and volutin. All the members are "algal" in organisation, being either unicellular or colonial. The cell-wall consists of a matrix of pectic substances strongly impregnated with silica, is always composed of several pieces and is commonly richly sculptured (fig. 1, F). No definite motile stages are known, but there is some slight evidence for their occurrence. This is a highly specialised class with a peculiar type of sexual reproduction (conjugation). Widely distributed both in freshwaters and the sea.

V. *Cryptophyceae*, with usually two large parietal chromatophores showing very diverse pigmentation (commonly some shade of brown). Pyrenoid-like bodies occur, but are often independent of the chromatophores; the products of photosynthesis are solid carbohydrates, in some cases starch, in others a compound akin to it. The motile cells (fig. 1, J) are pronouncedly dorsiventral, have two slightly unequal cilia, and possess a very specialised and characteristic structure. The majority of the members are of "flagellate" organisation and sexuality is only known in one form. The class is mainly marine and few forms are found in freshwater.

VI. *Dinophyceae* (*Peridinieae*), with usually numerous discoid, dark yellow, brown, etc. chromatophores, containing a number of special pigments. The products of photosynthesis are starch and oil. The majority of the members are "flagellate," but many possess a very elaborate envelope composed of a large number of often richly sculptured plates. The motile cells are provided with two furrows, the one transverse harbouring the transverse cilium, the other longitudinal constituting the starting-point for the longitudinal cilium which is directed backwards (fig. 1, E). Resting cysts of characteristic form are often produced. Sexual reproduction probable. The class is more widely represented in the sea than in freshwaters.

VII. *Chloromonadales*, with numerous discoid chromatophores having a bright green tint and containing an excess of xanthophyll. Pyrenoids are lacking and oil is the assimilatory

product. The few members of this class that are known are "flagellate," with two almost equal cilia (fig. 172). The class is restricted to freshwaters. Although superficially like Heterokontae, the detailed structure of the cells is altogether different.

VIII. *Euglenineae*, with pure green chromatophores, each cell usually with several. Pyrenoid-like bodies are present in some forms; the product of photosynthesis is a polysaccharide, paramylon, which occurs in the form of solid grains of diverse, and often very distinctive, shape. Only "flagellate" members are known and the majority are motile with the help of one or two cilia which arise from the base of a canal-like invagination at the front end (fig. 1, H). There is a complex vacuolar system. Only one case of sexuality is known. The class is practically confined to freshwater. It is highly specialised and its affinities are quite obscure.

IX. *Phaeophyceae*, with brown chromatophores containing, apart from the usual pigments, the yellow fucoxanthin. Pyrenoid-like bodies occur and oil is one of the storage-products. All the members are "algal," many with a very complex structure, and all but a very few are marine (Brown Seaweeds). The motile reproductive cells have two laterally attached cilia, of which one is directed forwards and the other backwards. No British freshwater representatives are known.

X. *Rhodophyceae*, with red, blue (especially among freshwater forms), etc. chromatophores containing, apart from the usual pigments, others like the red phycoerythrin and the blue phycocyanin. Pyrenoid-like bodies are often present and the product of assimilation is a polysaccharide, known as Floridean starch. Neither motile reproductive stages, nor "flagellate" members are known. The majority of the Rhodophyceae are marine (Red Seaweeds) and most exhibit a high type of organisation and a complex process of sexual reproduction.

XI. *Myxophyceae* (*Cyanophyceae*), with a simple type of cell (fig. 1, G), containing at best only a very rudimentary nucleus (central body) and with the photosynthetic pigments diffused through the peripheral cytoplasm; the usual pigments are associated with the blue phycocyanin and others to produce various tints, very commonly a blue-green one. Pyrenoids are lacking and the products of photosynthesis are sugars and glycogen. No "flagellate" members are known and motile stages are altogether lacking. There is no sexual reproduction. The members of this class are of simple organisation and exhibit simple methods of reproduction. They occur most abundantly in freshwater and terrestrial habitats, but are not uncommon in the sea.

It is quite probable that further research may necessitate an increase in the number of these classes; on the other hand, some slight evidence is accumulating for a nearer relationship between some of them (e.g. Chrysophyceae, Heterokontae, and Bacillariales[1]) and this may indicate a common origin in the remote past. Such views are briefly discussed under the appropriate classes in the main part of this book.

A reference to fig. 1 will show the essential characters of the type of cell, motile or otherwise, that is typical of most of these classes, but an adequate familiarity with each class is only to be obtained by a study of its chief members. The details of cell-structure are considered separately below (p. 32). In the first place it is well to undertake a consideration of

The Main Types of Construction encountered among the Pigmented Protophyta

The *motile unicell*, which is found in so many series (cf. fig. 1), is commonly a more or less spherical, oblong, or pear-shaped body, approximately circular in cross-section, although flattened dorsiventral types occur in several classes (cf. *Scourfieldia* (fig. 6, D, E); *Cryptomonas* (fig. 1, I, J); *Phacus* (fig. 173, H, I)). The extremity directed forwards during movement is spoken of as anterior and the opposite one as posterior. In most cases the organs of movement (flagella or cilia) arise at the anterior end, whilst the chromatophore or chromatophores occupy the posterior region or lie along the sides (cf. fig. 1). The nucleus is commonly situated near the middle of the cell. Where a cell-wall is present the surface-layer of the protoplast[2] is constituted by a plasma-membrane, but in the numerous naked types it is developed as a more or less rigid *periplast* that either admits of extensive change of shape (so-called *metaboly*, well seen in many species of *Euglena*) or gives the unicell a firm contour (*Cryptomonas* (fig. 1), *Phacus* (fig. 173, H, I)); it is distinguished from a cell-wall by the fact that it divides with the cell. The movements produced by the cilia vary somewhat in character, but are usually rapid. Many of the naked flagellate forms at times withdraw or shed their flagella and exhibit a creeping amoeboid movement, which is accompanied by marked change of shape and is only possible where the periplast is soft[3].

[1] cf. Pascher, 1921.

[2] The term protoplast is used to designate the living cell-contents, apart from the dead cell-wall.

[3] Such amoeboid movement also occurs at times in the reproductive cells of various Algae (cf. Pascher, Ber. Deutsch. Bot. Ges. xxvii, 1909, p. 143 and xxxvi, 1918, p. 352).

In many of the classes above distinguished there occur, side by side with the ordinary motile unicells, other types in which the cell is surrounded by a special, usually rigid and variously shaped envelope, provided with an apical aperture or apertures for the protrusion of the cilia and separated from the cell proper by a space (e.g. *Coccomonas* among Isokontae (fig. 13, N); *Chrysococcus* among Chrysophyceae (fig. 133, D); cf. also fig. 2, B). Such types may be spoken of as "*encapsuled.*" They occur both among forms in which the normal individual is naked, and among those in which it is provided with a cell-wall, and a considerable number of such organisms within the different classes (especially Chrysophyceae) have adopted an epiphytic habit (fig. 2, A). These sedentary forms either retain their cilia or lose them.

Another special development of the motile unicellular type is seen in the occasional *colourless forms* met with in certain series which, except for the absence of chromatophores, so closely resemble the pigmented forms that an undoubted affinity must exist (cf. *Polytoma* (fig. 4, F)). It is probable that with further research our knowledge of such secondarily colourless forms will be widely extended. Pascher[1] has described a number of members of Chrysophyceae and Dinophyceae in which the normal condition is amoeboid or rhizopodial (cf. p. 33), but such have not yet been observed in this country.

Further evolution of the free-moving individual has taken place in the direction of the *motile colony*. Here varying numbers of unicells are aggregated together in different ways within a mucous envelope to form flat plates (fig. 7, A) or more usually spherical groupings (fig. 2, C; fig. 9, A), in which all the individuals are alike and complete in themselves, although they do not normally occur separately; all contribute by the joint action of their cilia to the movement of the colony. Whilst in the majority of cases there is no appreciable differentiation among the individuals, a few Isokontae are known in which certain larger cells alone fulfil the reproductive functions, the others being purely vegetative (*Pleodorina* (fig. 10, A); *Volvox* (fig. 12, A)). Such colonial forms are scarcely to be distinguished from multicellular individuals (cf. p. 64)[2].

In a very large number of cases, however, especially among the forms showing "algal" organisation, motility has disappeared during the vegetative phase and is resorted to solely at times of reproduction. The beginnings of this tendency are plainly discernible among many of the free-moving unicellular types. Thus, in species of *Chlamydomonas* (Isokontae) and *Chromulina*

[1] Archiv f. Protistenk. xxxvi, 1915, p. 81; and xxxviii, 1917, p. 1 et seq.
[2] Regarding the concept of a coenobium, see p. 52.

(Chrysophyceae) the individuals at times lose their cilia and undergo successive division with a simultaneous development of mucilage-envelopes, so that there result big gelatinous masses comprising numerous cell-generations (fig. 4, I) and sometimes attaining sufficient dimensions to be plainly visible to the naked eye. These "*Palmella*-stages" are, in the case of the organisms just mentioned, merely temporary phases in the life-history, since sooner or later the contained cells acquire cilia and again adopt the swarming habit.

A large number of genera are known, however, in which this *palmelloid condition* is the permanent one (e.g. *Palmella* among Isokontae (fig. 2, E), *Chlorosaccus* among Heterokontae, *Chrysocapsa* among Chrysophyceae (fig. 138)), the reproductive cells alone exhibiting the swarming habit. All such forms are colonial, the individual cells, except for their aggregation within a common mucilage-envelope, being quite independent of one another and fulfilling all the functions of a living organism. The colonies are often of quite irregular and indefinite shape, like the *Palmella*-stages above mentioned, but in some cases the enveloping mucus possesses a definite form (*Apiocystis* (fig. 22), *Sphaerocystis* (fig. 16)). The mucilage is either secreted by the protoplasm of the constituent cells or arises by the gelatinisation of their membranes[1].

A variant of the type just considered in which the mucilage is produced locally, generally at the base of the cell, results in colonies which are *dendroid* in form, such as those of *Chlorodendron* (fig. 2, D) among Isokontae and *Colacium* among Euglenineae (fig. 174, A). In *Dinobryon* (Chrysophyceae) somewhat similar dendroid colonies are free moving (fig. 137).

In many of the motile unicellular types the individual comes to rest and draws in its cilia before division of the protoplast to form a new generation of free-moving unicells takes place. A prolongation of this sedentary phase, with an accompanying restriction of the swarming period, would lead ultimately to a motionless unicellular individual resorting to motility only at times of reproduction. This *chlorococcoid condition* is the permanent one in a very large number of Isokontae (e.g. *Chlorococcum* (fig. 23, C–F)) and is also encountered in many other classes (*Botrydiopsis* among Heterokontae (fig. 122, B), *Chrysosphaera* among Chrysophyceae (fig. 2, F, G), etc.). A further step in the same direction leads to the complete disappearance of motility, the reproductive cells being motionless from the first

[1] cf. Klebs, Unters. Bot. Inst. Tübingen, II, 1886, p. 333; Hauptfleisch, Zellmembr. u. Hüllgallerte d. Desmidiaceen, Diss. Greifswald, 1888; Schröder, Verhandl. Nat.-Med. Ver. Heidelberg, VII, 1902, p. 139.

and resembling the parent in all but size (azoosporic forms). Examples are seen in *Chlorella* (fig. 23, A, B), *Chlorobotrys* (fig. 128), etc.[1] The cells of the chlorococcoid types are commonly spherical, but other shapes are also realised. Among these unicellular sedentary forms there exists often a very strong colonial tendency, nowhere more highly developed than in the Isokontae where almost every conceivable type of motionless colony is to be met with; many of these colonies, in which the individuals are connected in various ways, possess a definite and distinctive shape (e.g. *Pediastrum* (fig. 28); *Coelastrum* (fig. 49); cf. also *Coelosphaerium* (fig. 185, A) among Myxophyceae).

It is a characteristic of all the types of Protophyte construction so far mentioned that, when cell-division occurs, the products of division of the protoplast, unless they remain permanently naked, sooner or later become completely invested by new cell-walls of their own. The membrane of the parent-cell is either ultimately cast off or, in some of the colonial forms, becomes mucilaginous. In other words cell-division in these cases leads to the formation of new units, which are quite independent of the membrane of the parent-cell, and is thus really solely concerned with reproduction. The more highly evolved forms, however, are characterised by a type of cell-division (*vegetative*) in which the parent-cell becomes septate, the two units produced by the division of its protoplast being merely separated by the development between them of a strip of membrane which is joined laterally to the membrane of the parent[2]. Among unicellular forms this type of cell-division is seen only in *Pleurococcus* (*Protococcus*) (fig. 86) and the doubtful genus *Chlorosphaera*[3] (fig. 23, H). It is however the rule in all the filamentous Algae which in fact owe their special habit to the adoption of this method of vegetative division (see especially, p. 142) and to its taking place ordinarily always in the same (transverse) plane. We thus obtain the *thread* or *filament*, a row of cells which are firmly connected with one another, and such simple filaments are found in *Ulothrix* (fig. 51, A), *Spirogyra*, etc., among Isokontae, in *Tribonema* (fig. 131, A) among Heterokontae, and in a large number of Myxophyceae (*Oscillatoria* (fig. 191), etc.). The filament is the simplest form of the *thallus*, as the multicellular plant-body of the Algae may be conveniently called.

Two modifications of this type of plant-body are frequent.

[1] See also Pascher, 1918.

[2] cf. however Pascher, Ber. Deutsch. Bot. Ges. XLII, 1924, p. 152.

[3] Although a modified process of division of this type prevails in Desmids, Diatoms, and many Chroococcales.

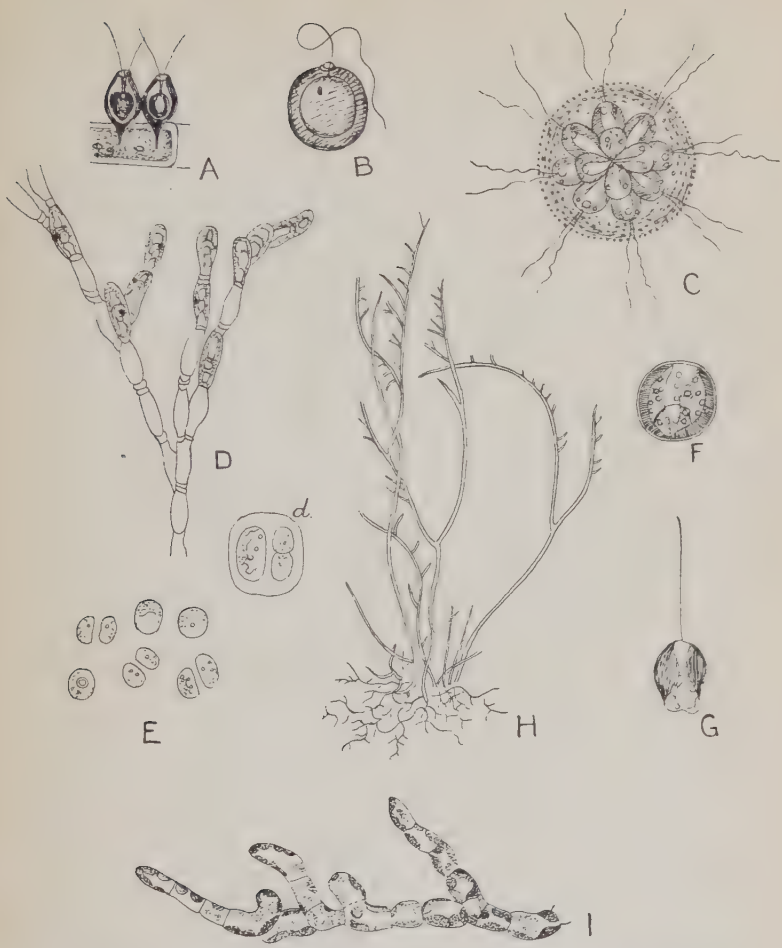

Fig. 2. Types of construction found among the pigmented Protophyta. A, *Chrysopyxis bipes* Stein (after Stein, ×490), encapsuled epiphyte. B, *Trachelomonas rugulosa* Stein (after Stein, × 490), encapsuled swarmer. C, *Syncrypta Volvox* Ehrenb. (after Stein, ×490), motile colony. D, *Chlorodendron subsalsum* (Davis), Oltmanns (after Davis, ×190), dendroid colony. E, *Palmella miniata* Leibl. (after Chodat), small part of a palmelloid colony; at *d* a stage in division. F–G, *Chrysosphaera nitens* Pascher (after Pascher): F, chlorococcoid cell; G, zoospore. H, *Stigeoclonium tenue* Kütz. (after Huber, from Oltmanns, inconsiderably magnified), branched filament with prostrate and erect systems. I, *Monocilia viridis* Gern. (after Gerneck, ×390), simple branched filament.

If septa are developed in more than one direction, we get flattened expanses, such as occur in *Prasiola* (fig. 61, G) and the Ulvaceae (fig. 59) among Isokontae, and in *Porphyra* among Rhodophyceae. Such a condition is very rare among freshwater Algae. More frequent is the development of a branching filament owing to the lateral outgrowth of more or less numerous cells, the outgrowths undergoing transverse septation like the main thread. Such branched filaments are to be found in all classes in which the filamentous habit has appeared and represent in many cases the highest type of development that has been reached. Examples are afforded by *Stigeoclonium* (fig. 2, II), *Phaeothamnion* (fig. 141), *Batrachospermum* (fig. 177), *Hapalosiphon* (fig. 205), etc. A peculiar form of false branching is found in many Myxophyceae (p. 436).

In many of the simpler unbranched filamentous forms all the cells are quite alike and every one is capable of growth and division and the formation of reproductive units. Such forms are little removed from colonies, except in the close association of their cells and in the fact that there is probably always some give and take at times of reproduction, since all the cells are rarely involved in the formation of spores or gametes, though potentially every one is capable of it. Moreover, in most cases such filaments, at least at first, tend to be attached to some substratum (other aquatics, pieces of wood or stone, etc.) by a specially modified basal cell (rhizoid)[1], which in the mature condition generally has a very scanty protoplast and is usually incapable of forming reproductive elements; these cells are often cemented very firmly to the substratum. Similar *haptera* are encountered in the branched filamentous types (e.g. *Cladophora*), but here there is often further-going division of labour. Thus, in some cases (*Cladophora*) growth and division are mainly restricted to the end-cells of the branches. In the more elaborate Algae (*Cladophora*, *Batrachospermum*) formation of reproductive cells is often practically confined to the ultimate branches, the principal (and sturdier) ones serving in the main only a supporting function. In *Draparnaldia* (fig. 70) among Isokontae and *Batrachospermum* (fig. 177) among Rhodophyceae the cells of the main axes are much larger and differ somewhat in form from those of the laterals and in *Draparnaldia* they have only a scanty chloroplast. In such cases therefore there is pronounced division of labour between the different parts of the filament.

Perhaps the most highly evolved type of filamentous plant-body is that which is characteristic of the Chaetophorales among

[1] cf. Borge, Ueber d. Rhizoidenbildung bei einigen fadenförm. Chlorophyc., Diss., Upsala, 1894; W. and G. S. West, Ann. of Bot. XII, 1898, p. 32.

Isokontae. Here the thallus consists of a prostrate creeping portion performing the functions of a holdfast, and, arising from it, branched filaments which trail out into the water (fig. 2, H). All possible stages in the relative development of these two parts are met with in the different genera (cf. p. 174). By a compacting of the filaments of the prostrate base and a complete disappearance of the erect system, flat attached discoid forms have originated, such as are excellently illustrated by the common species of *Coleochaete* (fig. 81); similar types are seen in *Hildenbrandtia* (fig. 180) among Rhodophyceae, and in many Chamaesiphonales (p. 465). The differentiation of the thallus into a prostrate and an upright system is encountered also in the simpler members of the Phaeophyceae (e.g. *Ectocarpus*) and Rhodophyceae, and it has been suggested[1] that from forms showing this type of construction the two alternating generations of higher plants may have diverged.

In a number of Algae considerable enlargement of the plant-body may take place without any septation occurring, so that a large multinucleate structure originates which is generally called a *coenocyte*. This *siphoneous* habit is most markedly developed among the marine Siphonales (Isokontae), but is well illustrated by the common *Vaucheria* (fig. 120) and is also seen in *Botrydium* (fig. 132) among Heterokontae. Such forms are best interpreted as multicellular structures lacking the usual septation.

In the classes Phaeophyceae and Rhodophyceae much more elaborate types of plant-bodies, with a bulky parenchymatous construction (cf. figs. 178, 179), have been developed, but in many cases these can be traced back to a simple filament. The bulk of the forms concerned are, however, marine and the few freshwater representatives of these classes show a relatively simple structure.

Attention has already been drawn above (p. 4) to the space-parasitism exhibited by a number of Algae belonging to different classes and to the symbiosis that sometimes exists between such forms and their "host." True parasitism is very much rarer, but is well seen in such tropical forms as *Phyllosiphon* and *Cephaleuros*[2].

In reviewing the types of construction encountered in the different classes one of the most striking facts that emerges is the parallelism of development exhibited in many cases. The

[1] Fritsch, New Phytol. xv, 1916, p. 233.

[2] cf. Kühn, Bot. Zeit. xxxvii, 1879, p. 322; Maire, Bull. Soc. Bot. France, lv, 1908, p. 162; Karsten, Ann. Jard. Bot. Buitenzorg, x, 1891, p. 24; Went, Zentralbl. f. Bakt., 2 Abt. i, 1895, p. 681.

motile unicell, the encapsuled type, the motile colony, the palmelloid, chlorococcoid, and filamentous types not only occur again and again, but quite analogous modifications of them are often to be found in different classes. With such facts before one it can hardly be doubted that evolution has progressed along similar lines in many, if not in all, series of Protophyta. Gaps are slowly filling up, but it is not to be expected that all the phases have been developed or preserved to the present day in every series. The table on p. 33 is intended to illustrate this parallel development, as far as it can at present be recognised, within six of the classes of Protophyta.

The General Organisation of the Cell among the Pigmented Protophyta[1]

The *shape of the cell* in the organisms under discussion is exceedingly varied. Among the unicellular and simpler colonial types the cells are often spherical, though not uncommonly there is elongation in one direction so that the cell comes to be oblong or ellipsoid (fig. 183) whilst still retaining a circular cross-section. This is also the usual form in the filamentous types where the cells are almost invariably cylindrical or barrel-shaped. Among the more specialised unicellular forms (Desmids, some Chlamydomonadaceae, *Cryptomonas*, *Phacus*) flattening of the cell may take place, so that the cross-section comes to be elliptical. In such cases the organism can be viewed from three aspects—the *front-view* when the broader face is presented to the observer (fig. 1, J; 6, D), the *side-view* when the narrower face is seen (fig. 6, E), and the more or less elliptical *end-view* (cf. e.g. fig. 1, I; 112, II). By contrast with the radial symmetry of most algal cells, such forms are isobilateral or, as in *Cryptomonas* (fig. 167, C), *Phacus*, and some Diatoms (e.g. *Epithemia* (fig. 163, B)) zygomorphic (with only one plane of symmetry).

In the majority of cases the cells are uninucleate, but multinucleate cells are found in a considerable number of the Isokontae (e.g. Hydrodictyaceae, Cladophoraceae) and numerous nuclei occur in the unseptate bodies of the siphoneous types (*Vaucheria*, etc.). Among the more advanced members that have been investigated the *nucleus* does not appear to differ in any appreciable respect from that of higher plants. Within the nuclear membrane are found a chromatin network and nucleolus lodged in the karyolymph, and in division the chromosomes result from the network, whilst the nucleolus does not make

[1] It is impossible to do more than survey the cytological structure cursorily in a work of this kind.

Type of Construction	Isokontae	Heterokontae	Chrysophyceae	Cryptophyceae	Euglenineae	Dinophyceae
(*a*) *Motile*[1] *unicell*	Chlamydomonas Carteria	Chloramoeba Heterochloris	Chromulina Hymenomonas Ochromonas	Cryptomonas Protochrysis	Euglena Phacus	Glenodinium Peridinium
(*b*) *ditto* (*encapsuled*)	Coccomonas Phacotus	——	Chrysococcus	——	Trachelomonas	——
(*c*) *Motile colony*	Gonium Pandorina	——	Chrysosphaerella Synura Uroglena	——	——	——
(*d*) *Dendroid colony*	Chlorodendron Hormotila	Mischococcus	Dinobryon (*motile*)	——	Colacium	——
(*e*) *Palmelloid*[2] *colony*	Palmella Tetraspora	Chlorosaccus	Chrysocapsa Hydrurus	Phaeococcus		——
(*f*) *Chlorococcoid* (*zoosporic*)	Chlorococcum Chlorochytrium	Botrydiopsis	Chrysosphaera	Tetragonidium	——	Cystodinium
(*g*) *Chlorococcoid* (*azoosporic*)	Chlorella Oocystis	Chlorobotrys	——	——	——	Hypnodinium
(*h*) *Simple filament*[3]	Ulothrix Microspora	Tribonema Bumilleria	Nematochrysis	——	——	——
(*i*) *Branched filament*[4]	Stigeoclonium Cladophora	Monocilia	Phaeothamnion	——	——	Dinothrix
(*j*) *Siphoneous*	Vaucheria Protosiphon	Botrydium	——	——	——	——
(*k*) *Rhizopodial*	——	——	Rhizaster	——	——	Dinamoeba

[1] Also in *Vacuolaria* (Chloromonadales).
[2] Also in many Myxophyceae (e.g. *Gloeocapsa*).
[3] Also in Oscillatoriaceae and Nostocaceae (Myxophyceae).
[4] Also in Phaeophyceae, Rhodophyceae, and some Myxophyceae (*Hapalosiphon*, *Stigonema*).

any obvious contribution towards them. This is the case for example in *Oedogonium*[1], *Coleochaete*[2], *Vaucheria*[3], etc. In many other cases (e.g. Volvocales[4], Chlorococcales[5], Conjugatae[6], some Rhodophyceae), however, the nucleus is characterised by a very poor development of the chromatin network, whilst the nucleolus contains much chromatin. In such nuclei, when stained, the nucleolus (here often called a *karyosome*) appears deeply coloured and surrounded by an almost clear zone occupied by the karyolymph in which a few linin threads may be apparent. In *Cladophora*[7] the nuclei may contain several karyosomes. In the division of this type of nucleus the chromosomes arise either entirely or in great part from the nucleolus, although according to Berghs[8] a part of the latter, in *Spirogyra*, is not used in this way and corresponds to the nucleolus of an ordinary nucleus. Nuclei of the two types occur in closely related forms; thus, whilst *Spirogyra* has a nucleus of the kind just described, *Zygnema* according to Kurssanow[9] has one of the ordinary type. No doubt transitions between the two also exist. Other special types of nuclei are referred to under the relevant groups (cf. especially pp. 395 and 409). The "central body" of the Myxophyceae is considered on p. 437.

The *photosynthetic pigments* of the cell are usually lodged in differentiated parts of the protoplast, known as *chromatophores*[10] (*chloroplasts* in Isokontae), and each cell may contain one or more of these bodies. They are most commonly situated in the lining cytoplasmic layer just beneath the cell-wall and are then said to be *parietal*. In quite a large number of the Isokontae, as well as in the Bangiales, however, the chromatophores occupy the central region of the cell and are said to be *axile*, though processes arising from them may extend for a considerable distance towards the periphery (cf. *Prasiola* (fig. 61, A–C), *Trebouxia* (fig. 23, K), many Conjugatae (fig. 100, 102, 103));

[1] Klebahn, Jahrb. Wiss. Bot. XXIV, 1892, p. 239; v. Wisselingh, Beih. Bot. Centralbl. XXIII, Abt. 1, 1908, p. 139.

[2] Allen, Ber. Deutsch. Bot. Ges. XXIII, 1905, p. 285.

[3] Kurssanow, Biol. Zeitschr. Moskau, II, 1912, p. 13; see abstr. in Just's Bot. Jahresber. 1913 (publ. 1921), 2 Abt. p. 1003.

[4] Zimmermann, Jahrb. Wiss. Bot. LX, 1921, p. 261.

[5] Bristol, Ann. of Bot. XXXI, 1917, p. 113; Smith, ibid. XXXII, 1918, p. 460.

[6] Kauffmann, Zeitschr. f. Bot. VI, 1914, p. 725; Acton, Ann. of Bot. XXX, 1916, p. 380; Berghs, La Cellule, XXIII, 1906, p. 55.

[7] Carter, Ann. of Bot. XXXIII, 1919, p. 475.

[8] Berghs, loc. cit. p. 64.

[9] Flora, CIV, 1911, p. 80.

[10] cf. Schmitz, Verhandl. nat. Ver. preuss. Rheinlande u. Westfalens, XL, 1883, p. 1; and Jahrb. Wiss. Bot. XV, 1884, p. 1.

in the same way a parietal chromatophore may show processes projecting into the interior of the cell (e.g. *Cladophora*). Apart from occasional exceptions, the cells in the majority of the simpler forms (cf. fig. 1) contain only one or two chromatophores, but these are often of distinctive and complex shape (e.g. fig. 93, 102, 157, D, E). In Algae possessing large cells (*Oedogonium*, fig. 87, A, *Cladophora*) the parietal chromatophore may become perforated to an appreciable extent so as to form a network. Numerous more or less discoid chromatophores are found in a parietal position in various Isokontae (*Dictyococcus*, *Eremosphaera* (fig. 31), *Vaucheria*), in many Heterokontae (cf. fig. 131, A), centric Diatoms (fig. 146, E), Peridinieae (fig. 168), etc. It is possible that the frequent dissection and perforation of the large chromatophores of the simpler forms indicates the way in which these small discs originated[1].

Apart from the special pigments which are present and which, as already indicated above (p. 21), constitute one of the bases of classification, the distinctive features exhibited by the chromatophores are often of great value in generic diagnosis. This will be readily apparent if the systematic portion of this book be consulted, and a further consideration is unnecessary at this point[2]. Attention may however be drawn to the fact that in a number of Algae the chromatophores are at times not at all well defined (e.g. *Scenedesmus*, *Hydrodictyon*, *Cladophora*), and this is the rule in the Blue-green Algae, where there has been much controversy on the subject (cf. p. 439). According to Carter[3] the accumulation of much starch in the chloroplasts of the Isokontae may lead to their becoming much swollen and to the obscuring of their natural outlines.

Associated with the chromatophores in several classes of Protophyta are bodies spoken of as *pyrenoids*[4] which consist of colourless masses of protein, usually of a rounded shape, though not uncommonly angular. In the Isokontae, where they have been most studied[5], they are embedded in the substance of the chloroplast and are enveloped by a sheath composed of small starch-grains which may be so closely aggregated that the individual grains are difficult to recognise. This pyrenoid-starch is of a more permanent character than that deposited

[1] cf. Oltmanns, Morph. u. Biol. d. Algen, III, 1923, p. 20; see however Carter, Ann. of Bot. XXXIII, 1919, p. 471.

[2] The special literature relating to the chromatophores is cited under the individual families and genera. With reference to the occurrence of chondriosomes (mitochondria) in Algae, see Guillermond, Rev. gen. Bot. XXVII, 1915, p. 277, and Moreau, Bull. Soc. Bot. France, LX, 1913, p. 123.

[3] loc. cit. p. 474, and Ann. of Bot. XXXIII, 1919, p. 222.

[4] Schmitz, loc. cit. p. 37.

[5] cf. also p. 55.

in the general stroma of the chloroplast and is the last to disappear under conditions of starvation. Pyrenoids are also known in Bacillariales, Cryptophyceae, Euglenineae, and Rhodophyceae, but it may be doubted whether they are all of the same nature as those of the Isokontae, though they are probably analogous structures. In Diatoms they often form prominent bulges on the inner surface of the chromatophore, whilst in Cryptophyceae they commonly occur independently of the latter (fig. 167, p. 390). The pyrenoids of these forms are frequently "naked," i.e. devoid of a special sheath, and this is also the case in some Isokontae. Pyrenoids have not been observed in the large classes Heterokontae, Chrysophyceae, and Dinophyceae.

Pyrenoids are usually regarded as stores of reserve-protein, but they often show a curious degree of permanence which is not altogether in harmony with this view. The fact that in many cases the pyrenoids disappear more or less completely during the formation of reproductive cells may indicate that they (and the carbohydrate reserves which are often associated with them) are utilised more particularly for the development of such structures. Pyrenoids may be present or absent in closely related forms, whilst in some species their occurrence is variable (e.g. *Debarya calospora* (Palla) W. & G. S. West). In spite of this, however, the possession of pyrenoids, their number, and their position within the chromatophore afford features which are of considerable value for taxonomic purposes[1].

In many of the free-moving unicells and colonies, as well as in the reproductive swarmers of various Algae, there is found usually nearer the anterior end of the cells, a reddish or brownish-red dot or streak, the *eye-spot* or *stigma* (cf. figs. 1, 3, D, 4). A similar structure is present in many colourless motile organisms, both of the Vegetable and Animal Kingdoms. As a general rule the eye-spot is apposed to the edge of the chromatophore or, if several chromatophores are present, to one of them. In *Euglena* (fig. 173, *s*) and Dinoflagellata (fig. 1, E), however, it occupies an independent position. The accounts of its structure are somewhat conflicting[2]. It would seem that the red pigment is lodged in a slight thickening of the plasma membrane and in some cases at least a colourless lens-like body lies below (*Cladophora*) or

[1] The special pigmentation of the chromatophores and the assimilatory products associated with them are dealt with under the different classes in the special portion of this book.

[2] Strasburger, Histol. Beitr. VI, 1900, p. 193; Francé, Archiv f. Hydrobiol. u. Planktonk. IV, 1909, p. 37; Rothert, Ber. Deutsch. Bot. Ges. XXXII, 1914, p. 91. The last regards the eye-spot as a modified chromatophore, which certainly seems correct in the case of the swarmers of Phaeophyceae.

above it (*Gonium*)[1]. It is usually assumed that the eye-spot is an organ for the perception of light, but the experimental evidence in support of this suggestion is inadequate—in particular the absence of an eye-spot in many motile forms would seem to indicate that it cannot be of paramount importance.

The *flagella* or *cilia*, by means of which movement is effected in the motile types, are prolongations of the cytoplasm. It has been usual to call the finer organs of the Algae cilia, and the coarser ones found in many Flagellata flagella, but it may be doubted whether the distinction is one that can be maintained on a scientific basis. It has been shown that the coarser flagella of many forms possess a rather complicated structure[2], but regarding the cilia of most Algae nothing is known. It would seem that a distinction can often be drawn between a more rigid tubular basal portion and a highly flexible distal portion which is regarded as the prolongation of an axial thread traversing the former. In many groups, where the swarmers have more than one cilium (e.g. Heterokontae, Cryptophyceae), they are differently orientated (cf. fig. 1) and appear to have different functions, whilst in Peridinieae the two cilia not only differ in these respects (fig. 1, E), but seem to have a different structure[3].

In many cases the cilia emerge from a specially differentiated part of the protoplast (Strasburger's *kinoplasm*) which arises as a thickening of the plasma-membrane and is well seen in the multiciliate zoospores of *Oedogonium* (fig. 88, B) and in those of *Cladophora*. The same structure seems to occur in the swarmers of many other Isokontae, and the little variously shaped beaks ("Membranwarze" of the Germans) that project between the cilia in many species of *Chlamydomonas*, etc. (cf. fig. 73, H, I) are probably occupied by cytoplasm of the same nature. It is not, however, at present clear whether there is in all motile types such specially differentiated cytoplasm at the point of origin of the cilia. It has been shown in a considerable number of forms that the bases of the latter are occupied by readily stainable granules; sometimes two or more cilia arise from a common granule. Such *basal granules* have been identified with *blepharoplasts*, but their general occurrence in motile Protophyta is still in doubt. In *Euglena*[4], *Polytoma*[5], etc., the basal granules are connected by special cytoplasmic strands with other granules located near the nucleus.

[1] Mast, Journ. Exper. Zool. xx, 1916, p. 6.

[2] Fischer, Jahrb. Wiss. Bot. xxvi, 1894, p. 187; Dellinger, Journ. of Morphol. xx, 1909, p. 171; Oltmanns, loc. cit. iii, p. 95.

[3] cf. p. 393. [4] Haase, Archiv f. Protistenk. xx, 1910, p. 49.

[5] Entz, ibid. xxxviii, 1918, p. 329.

The movements of the cilia are apparently in most cases very complex[1] and have only been studied in relatively few forms. In the vast majority of cases the motile cell or colony rotates upon its own axis during its forward progression, but other types of motion are seen in *Cryptomonas* (cf. p. 391) and *Scourfieldia*[2].

Like that of other plant-cells the protoplast of the organisms under discussion is usually provided with one or more large *vacuoles*. Exceptions are afforded by *Prasiola*, *Pleurococcus*[3], and many Blue-green Algae. Not uncommonly there is a large central sap-vacuole and the cytoplasm forms a parietal layer beneath the cell-wall. In many of the simpler free-moving Isokontae there is an axial cytoplasmic strand containing the nucleus and extending from the posterior pyrenoid to the bases of the cilia at the front end.

In motile cells, and occasionally in sedentary types (e.g. *Asterococcus* (fig. 17, II, *cv*)), there occur so-called *contractile vacuoles*[4] of which there may be one or many (often two). These structures, though constant in position, exhibit a periodic contraction of the plasma-membrane (tonoplast of De Vries), whereby their fluid contents are discharged into the surrounding cytoplasm. The contraction is usually a sudden one, but the subsequent enlargement takes place slowly (occupying from 15 secs. to a minute); often the vacuole disappears completely at the time of contraction, but in other cases it only undergoes diminution in size. Where only two such vacuoles are present, they generally expand and contract alternately. In many of the flagellate forms (Chrysomonadales, Cryptomonadales, Euglenineae) there is a complex arrangement of contractile vacuoles emptying into a central reservoir (cf. especially fig. 172, B, C); in some cases (e.g. Euglenineae) this appears to discharge into a special canal-like invagination of the anterior end of the protoplast (fig. 173). The exact function of contractile vacuoles is still a matter of doubt; many regard them as an excretory mechanism.

In many of the smaller Algae the *cell-wall* is a thin and delicate structure, but in the larger forms it tends to be more robust and in such cases a number of layers can usually be distinguished. Superficially there is a denser, darker-looking layer which is generally spoken of as a *cuticle*, but little is known as to its chemical nature, although it shows itself resistant to many reagents. In filamentous forms the "cuticle" is confined to the

[1] cf. especially Ulehla, Biol. Centralbl. XXXI, 1911, p. 645 et seq.
[2] West, 1912, p. 327.
[3] Fritsch, 1922, p. 14.
[4] Pfeffer, Abh. mat.-phys. Kl. sächs. Ges. Wiss. Leipzig, XVI, 1890, p. 336.

free surfaces of the cells and often appears continuous over considerable stretches. The remainder of the cell-wall in many Isokontae consists largely of a cellulose-like compound, giving a blue reaction with iodine and sulphuric acid or with chlorzinc-iodide. In other cases (e.g. Heterokontae) it is composed of pectic substances (staining with ruthenium red) and the same occur as the basis of the wall in Diatoms, where however there is a rich impregnation with silica. It is evident that many other compounds play a part in the formation of the algal cell-wall, but our knowledge of these matters is still in its infancy. Thickened walls are often markedly stratified (Cladophoraceae (fig. 63. D), *Trentepohlia*). Not uncommonly inorganic substances are deposited in or on the wall, e.g. the deposits of lime found in the Desmid *Oocardium* (fig. 116. D–E) and in various Myxophyceae, and the iron compounds frequent in the membranes of some Desmids, species of *Trachelomonas*, etc. As a general rule the cell-wall consists of a single piece, but in Desmids, Diatoms, and many Heterokontae the wall is composed of two overlapping pieces, which are sometimes of unequal size.

The mucilage-envelopes and mucilage-accumulations found in so many Protophyta[1] are in part modifications of the cell-wall, but in a large number of cases represent secretions of the protoplast, which, in the case of Desmids and Diatoms for instance, are emitted through definite pores in the membrane (pp. 255, 344). They fulfil very diverse functions, viz. to hold the individuals of colonial forms together, as a protection against desiccation in many terrestrial Algae, as a means of movement in some Desmids, etc. Their form is very diverse and in some cases they show marked stratification (fig. 18, E; 187, C–E) or a fibrillar structure. Filamentous Algae, like *Spirogyra*, which are provided with a mucilage-envelope, are not generally inhabited by epiphytes.

Little can be said here about cell-division, the more so as details relating to special groups will be found in later sections. The division of the nucleus does not in many Protophyta differ fundamentally from that of higher plants. As a general rule it would appear to take place at night, although many exceptions are known. The nuclear spindle is formed in the usual way in most of the forms that have been studied, but in *Euglena*[2] it is lacking and the chromosomes merely group themselves about the elongating nucleolus, which ultimately constricts into two halves as the chromosomes separate into two groups. In multi-

[1] See the literature cited in footnote 1 on p. 27.

[2] Keuten, Zeitschr. Wiss. Zool. LX, 1895, p. 215; Tschenzoff, Archiv f. Protistenk. XXXVI, 1916, p. 137.

cellular forms the septum between the two daughter-nuclei most commonly arises practically independently of the nuclear spindle, as an annular ingrowth from the wall of the parent-cell which gradually extends across the latter till the protoplast is divided into two. This method of septum-formation is met with both in forms with uninucleate cells (e.g. *Spirogyra*), as also in the multinucleate cells of Cladophoraceae. Cases are however also known in which the separating wall is formed simultaneously[1]. The division of the protoplast is accompanied by a division of the chromatophores which may take place at an earlier or later stage. The pyrenoids frequently divide at the same time, but in many forms they disappear during cell-division to reappear in each daughter-cell when the process is complete. Eye-spots and contractile vacuoles behave in the same way.

In many filamentous Algae in which the septa become more or less appreciably thickened, obvious pits are formed within them (e.g. many Rhodophyceae (fig. 176, D), *Trentepohlia*, etc.). The pit-membrane in such cases is probably traversed by plasmodesmae, but such have only been demonstrated in a few forms (e.g. *Volvox*)[2]. Conspicuous protoplasmic connections are also observed in some Blue-green Algae (fig. 206). In a large number of the simpler filamentous Isokontae with relatively thin septa there is at present no evidence for the existence of any connection between the protoplasts of adjacent cells.

The Reproductive Processes

The processes of reproduction encountered in the Protophyta may be considered under three headings,—vegetative, asexual, and sexual. The treatment at this point is only of a general nature and for details the individual classes and genera should be consulted.

Vegetative reproduction. It is legitimate to class as vegetative all those processes of reproduction in which portions of the plant-body become separated off to give rise to new individuals without any obvious changes in the protoplasts. Common examples are afforded by the breaking up of the threads of many filamentous Algae into short lengths (so-called *fragmentation*, cf. fig. 57), whereby prolific multiplication often takes place resulting in the extensive tangles, known popularly as *pond-scums*. A more special case is the *hormogone*-formation met with in the filamentous Blue-green Algae (cf. p. 446), and here constituting the chief method of reproduction. One can include in

[1] e.g. *Trentepohlia* (cf. Brand, Beih. Bot. Centralbl. XII, 1902, p. 204); also Oedogoniales (cf. p. 214).

[2] Meyer, Botan. Zeit. LIV, 1896, p. 192.

the same category the mode of multiplication of many colonial forms by the splitting of the mature colonies into two or more parts (e.g. *Dictyosphaerium*, *Synura*, *Microcystis*, cf. also fig. 136, A). The vegetative divisions of a *Pleurococcus*, of Desmids, and of many unicellular Blue-green Algae are essentially of the same kind, as also is the longitudinal division of most naked Flagellates.

A more specialised type of vegetative reproduction is seen in relation to the formation of structures which are to tide over a period unfavourable for ordinary vegetative development. In these cases the cells involved undergo thickening of their membranes and at the same time plentiful reserves (oil, starch) accumulate within the protoplast; in some cases special pigments are formed, so that the cells assume a distinctive (often red) tint. Such structures are called *akinetes*[1] and are most typically developed in the filamentous forms (cf. fig. 53, I). Usually the cells thus modified ultimately round off more or less and separate from one another, so that each constitutes a distinct reproductive unit, but in *Cladophora* and certain other forms this is not the case and rows of cells that have assumed this character during winter give rise later to new growth without falling apart. A special mode of akinete-formation, in which only a part of each parent-cell is used, is distinctive of the genus *Pithophora* (fig. 65). The spores of Myxophyceae (fig. 197) can likewise be regarded as specialised akinetes (see also p. 44).

Asexual reproduction[2]. The commonest method of asexual reproduction is by means of *zoospores*. These are ordinarily naked ciliate protoplasts, which have been formed by a rejuvenescence of the parent's cells[3]. The first step in the development of zoospores seems in all cases to be a slight contraction of the protoplast away from the cell-wall. Only a single zoospore may be formed from the contents of each cell (*Oedogonium* (fig. 88); *Microspora* (fig. 52, C), etc.) or, more commonly, division of the contents into two, four, eight, or more parts (several hundred in *Cladophora*) takes place and an equivalent number of zoospores is produced. In the majority of the Algae the cells from which the zoospores are formed are not specially differentiated, but in *Trentepohlia* (fig. 3, B, C, G) and its allies certain cells become modified to form zoosporangia and the production of zoospores is confined to these. Liberation of the zoospores

[1] Wille, 1887, p. 492.

[2] It is not of course possible to draw a hard and fast limit between vegetative and asexual reproduction.

[3] cf. Berthold, Protoplasmamechanik, Leipzig, 1886, p. 291; Strasburger, Hist. Beitr. IV, 1892, p. 62; Pascher, Bibliotheca Botanica, LXVII, 1907.

may take place through a specially prepared hole in the wall (many Ulotrichales (fig. 51, B)), by breaking open of the wall at one point (*Oedogonium* (fig. 88)), or by disrupture of the cell (*Tribonema* (fig. 131)). In many cases the zoospores at the moment of their liberation are surrounded by a delicate vesicle of a mucilaginous character (fig. 51, B), but this is of quite a temporary nature and disappears after a few seconds.

Where numerous zoospores are formed from a cell, the fission of the protoplast may either take place successively (*Ulothrix*) or simultaneously (*Hydrodictyon*, *Sorastrum*). In such cases it would seem that, as a rule, the superficial plasma membrane and that bounding the central vacuole are not utilised in the production of the zoospores. Zoospores of a very peculiar type are characteristic of *Vaucheria*. The large multiciliate swarmer (fig. 3, A) formed within the special terminal zoosporangium is probably to be regarded as a compound zoospore constituted by a large number of units that do not separate, since it includes the central vacuole and cilia arise in pairs opposite each nucleus.

Zoospores would appear normally to be produced at the height of vegetative activity and commonly at night. The investigations of Klebs (1896) have shown that in many filamentous forms a change in external conditions acts as a stimulus to zoospore-formation, e.g. transference from flowing to still water (*Ulothrix*, *Oedogonium*), change of illumination, transference to water (in the case of terrestrial Algae like *Hormidium* and *Vaucheria*), etc. Light always appears to inhibit zoospore-formation and transference to a dark place or even into a diminished light-intensity often calls forth the production of swarmers. In many cases algal material that is brought indoors and kept healthy proceeds after a very short time to give rise to zoospores.

The latter appear generally to show marked phototactic irritability, moving towards light of medium intensity, but being repelled by intense light[1]. Various Ulotrichales and Chaetophorales produce two kinds of zoospores with different phototactic sensitiveness (p. 144). The duration of movement is only known for a few forms, but appears to vary within wide limits in different Algae (between half an hour and a couple of days). Towards the end of the period of movement the zoospores of most filamentous and other sedentary forms seek out dark objects upon which they come to rest. As a general rule it is the anterior end of the zoospore that becomes fastened to the substratum; this is followed by the withdrawal of the cilia and

[1] Strasburger, Jenaische Zeitschr. XII, 1878, p. 551. The same features are exhibited by motile colonies (e.g. *Volvox*, cf. Oltmanns, Flora, LXXV, 1892, p. 183).

the secretion of a cell-membrane, whilst the attached end broadens out into a variously shaped holdfast (cf. fig. 87, B).

The zoospore affords a ready means of rapid dispersal within the fluid medium at times of rich vegetative growth. In the case of motile forms with an "algal" organisation (e.g. Chlamydomonadaceae) the production of new individuals by the successive division of the protoplast into two, four, or eight parts is quite of the same character, except that in this case the swarmers are provided with cell-walls from the time of their liberation and the naked phase is passed only within the parent-cell and is of brief duration. Of essentially the same nature is the fission of

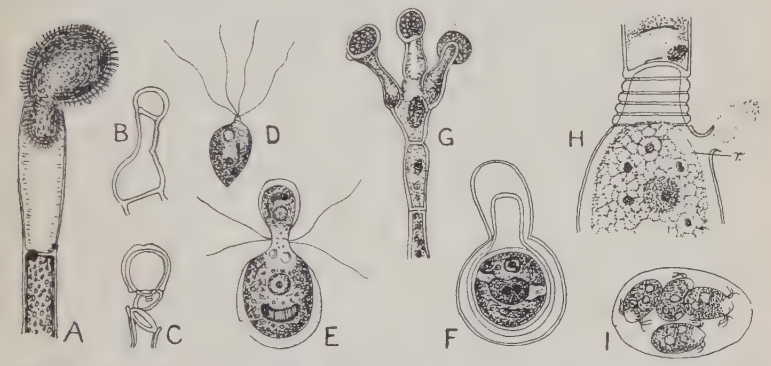

Fig. 3. Asexual and sexual reproduction in the Algae. A, *Vaucheria repens* Hass., liberation of zoospore (after Goetz). B and C, *Trentepohlia Iolithus* (L.) Wallr., sporangia (after Brand, ×240); C, shows detachment of sporangium. D, *Ulothrix zonata* Kütz., zoospore (after Klebs, ×300). E–F, *Chlamydomonas monadina*, Stein, sexual fusion (after Goroschankin, E ×450; F ×600). G, *Trentepohlia aurea* (L.) Mart., thread with sporangia (after Gobi). H, *Oedogonium Boscii* Wittr. (after Klebahn), mature oogonium, showing ovum with receptive spot (*r*). I, *O. pluviale* Nordst., germination of oospore (after Juranyi, ×270).

the motile naked individual of a *Chromulina*, *Euglena*, etc., above referred to under vegetative reproduction.

In many zoosporic forms it happens occasionally both in nature and under conditions of culture that, after the preliminary steps have occurred and the zoospores are all but formed, a rounding off of the protoplasts takes place and a cell-wall is secreted around each. Such structures, which are to be regarded as arrested zoospores which have skipped the motile phase, are termed *aplanospores*[1] (fig. 131, B and I). In some cases their membranes undergo thickening and the resulting cells, which are capable of a prolonged resting period, are then known as

[1] Wille, 1887, p. 492.

hypnospores. All such structures are liberated sooner or later by the breaking open of the membranes of the parent-cells.

In a large number of Algae (many Chlorococcales) production of zoospores never takes place, but reproductive cells are formed, with or without division, by rejuvenescence of the protoplast; new cell-walls independent of those of the parent are then formed around the products, just as in aplanospore-development. It is probably legitimate to suppose that, in many cases at least, such forms have been derived from a zoosporic ancestor, but have adopted permanently the aplanosporic condition. The resulting daughter-cells in many of these Algae are absolute miniatures of the parent and acquire all the distinctive features (sculpturing of the wall, special outline, etc.) whilst still enclosed in the parent-cell (cf. figs. 27 : 37, C : 38, A). In such cases one speaks of *autospores* and especially good instances are to be found in many Chlorococcales. The term autospore can be extended even to motile individuals which acquire the mature form, etc., before liberation (cf. *Brachiomonas* (fig. 6, J)).

Of a comparable nature are the "*gonidia*" formed in certain Myxophyceae (p. 448) and the *monospores* (fig. 176) and *tetraspores* of Florideae. A common method of asexual reproduction in many filamentous Myxophyceae is by means of *spores* (figs. 197, 203, A) which are however more of the nature of akinetes. They are produced from single vegetative cells which frequently undergo appreciable enlargement and marked thickening of the membrane. These structures, like the akinetes and hypnospores already mentioned, are resting-stages, often capable of remaining dormant for very long periods without loss of vitality.

The *cysts* which constitute the resting-stages of most flagellate forms are in so far peculiar that in their production a definite membrane, not present in the ordinary vegetative condition, is secreted. Encystment takes place very readily in some cases (e.g. *Euglena*). In the Chrysomonadales (p. 315, and fig. 133, F) and Peridineae (fig. 171, B) the cysts are of an exceedingly characteristic type.

Sexual reproduction. The occurrence of sexual reproduction probably marks a relatively advanced stage of evolution among Protophyta, since this process is lacking in whole classes (Myxophyceae, Chrysophyceae) and is very rare in all the types that are regarded as of relatively low organisation (Polyblepharidaceae, the simpler Heterokontae, etc.).

In many of the simpler Isokontae the sexual cells or *gametes*, which are always uninucleate, are not differentiated from one another and the forms in question are described as *isogametes* (e.g. *Chlamydomonas* fig. 5, D, E), *Ulothrix*, *Monostroma* (fig. 39,

F–H, etc.)). In such cases the gametes originate by a division of the protoplast of the parent-cell into a number of small portions which are liberated in the same way as the zoospores. Such gametes are in fact outwardly often only distinguished from the zoospores by their smaller size, although there are sometimes differences in the number of the cilia and in other respects. Except in a few species of Chlamydomonadaceae the gametes are always naked. As a general rule they develop in the ordinary vegetative cells, though special *gametangia* are found for instance in *Trentepohlia*. The fusing gametes usually become entangled by their cilia and either meet end to end (fig. 5, E) or become laterally apposed to one another (fig. 59, G). The product of fusion (zygote) often continues to move for a little time with the help of the cilia of the two gametes from which it has been produced (fig. 59, H), but soon rounds off and comes to rest (fig. 59, J). There are a considerable number of records testifying to the fact that attraction only exists between gametes from distinct individuals and that such alone undergo sexual fusion. This implies that, although morphologically similar, there are physiological differences between the sexual cells, even in these isogamous forms.

In a considerable number of isogamous Algae slight differences in the size of the two fusing gametes have frequently been observed, but this has become a fixed character in certain species and genera which are then described as *anisogamous* (*Chlamydomonas monadina* (fig. 3, E, F); *Pandorina, Aphanochaete* (fig. 67)). The larger gamete is generally more sluggish in its movements and frequently comes to rest after a short time, being sought out by the more active smaller gamete. In *Chlamydomonas coccifera* Gorosch. the larger gamete is constituted by an ordinary cell which loses its cilia and increases in size.

Such cases lead over to the *oogamy* which is met with in several advanced types of Isokontae. Here a large motionless female cell or *ovum* is fertilised by a much smaller active male cell or *spermatozoid*. In *Sphaeroplea* (fig. 66, E) the two types of gametes are formed in the ordinary vegetative cells, but in most oogamous Algae they are produced in special cells, the sexual organs. Of these the female or *oogonium* is usually enlarged and invariably develops but a single ovum (figs. 3, H; 121, A, *oo*), while the male or *antheridium* gives rise to any number of male cells which are ciliated and very active in their movements. While the ovum is usually provided with one or more chromatophores and plentiful food-reserves, the spermatozoids generally harbour only a small inconspicuous, often yellowish, chromatophore and are destitute of food-stores.

It is characteristic of all freshwater Algae that the ova are retained within the oogonium, access for the fertilising spermatozoid being provided by the development of an aperture in the membrane of the latter (cf. figs. 58, B; 90, C), through which at the time of maturation of the ovum a certain amount of protoplasmic slime is often exuded (figs. 3, II; 121, A). The part of the ovum nearest the aperture commonly exhibits a colourless cytoplasmic area, the *receptive spot*, and it is here that the penetration of the spermatozoid takes place. In *Coleochaete* the oogonium is provided with a long neck, the tip of which breaks down to allow of the entry of the spermatozoids which in this genus are sometimes completely colourless.

All the known members of the Red Algae exhibit an oogamous sexual process of a very specialised kind. The spherical male cells (*spermatia*) are formed singly within the antheridia (fig. 175, C) and are invariably motionless. They are conveyed passively by water-currents to the long neck or *trichogyne* of the female organ (cf. fig. 175, B and A). A complete absence of motile power on the part of the fusing gametes is also characteristic of Conjugatae and Diatoms, where however isogamy usually obtains (see pp. 224 and 345).

Where sexual differentiation occurs, the two types of sexual cells are either developed on the same individual (the *monoecious* condition, seen in some species of *Volvox* (fig. 12, A), *Oedogonium* (fig. 89), etc. and the rule in *Vaucheria* (fig. 121)) or on distinct individuals (the *dioecious* condition). It would seem that, as a general rule, the production of sexual cells ensues when a considerable accumulation of nutritive materials has taken place and there is some check to vegetative growth. Klebs (1896) showed clearly that bright light is of major importance in stimulating the production of gametes and this conclusion is also supported by direct observation in nature[1]. It is probable however that most Algae require to be in the right state, and it is only when that is the case that light acts as the determining stimulus. According to Transeau[2] vegetative growth must go on for a certain time before reproduction is possible and the speed of the metabolic processes must attain a certain minimum rate or reproduction fails to occur. He finds that in *Spirogyra* (and probably also in *Oedogonium*) the time-interval elapsing between the first appearance of a species and the commencement of sexual reproduction depends on the temperature and the specific surface (i.e. total surface divided by volume). In nature sexual reproduction usually coincides with the time of maximum

[1] Fritsch and Rich, 1913, p. 68; cf. also Hodgetts, 1921, p. 23.
[2] Amer. Journ. of Bot. III, 1916, p. 126.

abundance of an Alga and very often, though not always, it marks the end of the period of active growth and is followed by more or less complete disappearance of the form involved. In many cases too it coincides with a low water-level, when relatively high concentrations of the water tend to occur[1].

The product of sexual fusion (zygote) usually becomes enveloped sooner or later in a membrane which, in most cases, undergoes considerable thickening and frequently develops a characteristic sculpturing or becomes beset with spines, warts, etc. (figs. 66, B; 104, C). The contents are laden with food-reserves and frequently harbour quantities of a yellowish-red oil. The resulting structures are spoken of as *zygospores* when they are the products of an isogamous or anisogamous fusion, and as *oospores* in the case of oogamous types. In most fresh-water Algae zygospores and oospores constitute resting-stages in the life-cycle, although this is not so in the Rhodophyceae. In *Coleochaete* the oospore becomes encased in an envelope formed by the outgrowth of threads from the adjacent cells of the gametophyte, but this is the only case of the kind met with in freshwater Algae (cf. fig. 68, A, *o*).

The fusion of the cytoplasm of the gametes is accompanied by a fusion of the nuclei, which may either ensue almost immediately or be more or less appreciably delayed; in many Conjugatae nuclear fusion is apparently postponed until the time of germination of the zygospores[2]. In many isogamous forms the chromatophores contributed by either gamete seem to persist in the zygote[3], although in the case of *Spirogyra*[4] those of the male gamete (cf. p. 236) disintegrate soon after fusion. In oogamous forms the chromatophore-content of the oospore is likewise entirely derived from the female cell, since the male gametes at most include but a very reduced chromatophore. The young zygote of Isokontae usually harbours appreciable quantities of starch, most or all of which is subsequently converted into the fat which forms the principal food-reserve in the resting spore and is gradually used up during the first stages of germination.

Among isogamous forms the sexuality of the gametes is often not very pronounced and, in the absence of fusion, they may at

[1] cf. Hodgetts, 1921, p. 7. Transeau's results for Illinois (Trans. Amer. Microscop. Soc. xxxii, 1913, p. 37) would hardly apply to smaller pieces of water in this country.

[2] Klebahn, Ber. Deutsch. Bot. Ges. vi, 1888, p. 160; and Jahrb. Wiss. Bot. xxii, 1891, p. 420.

[3] cf. for instance Dodel, Jahrb. Wiss. Bot. x, 1876, p. 501, 517; Pascher, Ber. Deutsch. Bot. Ges. xxxiv, 1916, p. 234.

[4] Tröndle, Bot. Zeit. lxv, 1907, p. 196.

times behave as zoospores and give rise to new plants. In the more specialised types, however, the sexual cells are generally incapable of further development, if they fail to achieve a union. As a matter of fact very few examples of *parthenogenesis* (development of an ovum without fertilisation) are known among freshwater Algae, although in various cases such parthenogenesis has been induced by experimental means (cf. pp. 237 and 292)[1].

The *germination* of the sexually produced spores has so far only been observed in relatively few cases, although data exist with respect to this point for most of the genera in which sexuality occurs. It is a significant fact that, with very few exceptions (e.g. *Vaucheria*), the zygospores or oospores as the case may be do not give rise directly to a new generation. During germination the nucleus divides two or more times, and this is usually followed or accompanied by a division of the protoplast leading to the formation of a number of asexual reproductive cells, which are liberated by rupture of the thick membrane, and each of which can form a new individual. In various Isokontae the zygote in germination gives rise to zoospores which, after a period of swarming, produce the new plant in the usual way (*Oedogonium* (fig. 3, I), *Ulothrix*). Among Conjugatae, where two nuclear divisions invariably occur in the germinating zygospore, one (Zygnemales), two (Desmids), or four (Mesotaeniales) individuals may result, the unused nuclei gradually degenerating. Except among the Bacillariales, where quite special conditions obtain (p. 346), the first nuclear division in the zygote is probably always a reduction-division, although the actual fact has only been demonstrated in a very limited number of cases.

The diploid[2] phase in the life-cycle is thus in all freshwater Algae (excluding Bacillariales) restricted to the zygospore or oospore and, regarded purely from the cytological standpoint, these are the only phases comparable with the sporophyte of the higher plants. This sporophyte can be interpreted as comprising merely a sporangium within which are produced spores giving rise to the ordinary phase, the gametophyte (haploid[2] generation). In so far as one accepts such an interpretation, most sexually reproducing freshwater Algae may be said to show slight indications of antithetic *alternation of generations*.

In *Coleochaete* among Isokontae and in the Nemalionales[3]

[1] A convenient summary is given by Winkler (Progressus Rei Bot. II, 1908, pp. 305, 387).

[2] The diploid phase has nuclei with twice as many chromosomes as the haploid phase.

[3] Many of the marine Rhodophyceae exhibit a more complex alternation, differing from that of the freshwater forms here described (cf. p. 420).

among the Rhodophyceae, however, the oospore undergoes a more or less extensive vegetative development before proceeding to form the reproductive cells that give rise to the gametophyte. In *Coleochaete* the oospore divides into 8 or 16 cells, each of which produces a zoospore (fig. 68, B), whilst in the Nemalionales the fertilised carpogonium puts forth a number of short filaments (fig. 175, A), some of whose cells form the *carpospores* which give rise to a new thallus. In these special cases, as far as our knowledge goes, the reduction-division takes place at the same point in the life-cycle as in other freshwater Algae, so that the vegetative development of the oospore is cytologically but a phase of the gametophyte. Some authorities have however been inclined to regard these Algae as showing a more advanced type of sporophyte, in which reduction still takes place at the commencement instead of at the end of the sporophytic phase[1].

Although the meeting together of the sexual cells in the case of most of the Algae depends upon chance, the customary growth of the forms concerned in dense communities no doubt renders sexual fusion easy of accomplishment. At the same time, since various species and genera usually occur intermingled, the production of *hybrids* is to be expected. That, so far, little is known of hybrids among freshwater Algae is no doubt due to our imperfect knowledge of most algal species and to the lack of consecutive observation of algal forms as they occur in nature. Hybrids have however been recorded in *Spirogyra*[2], and Pascher[3] has carried out experiments on hybridisation in *Chlamydomonas*. His methods may well give scope for a more detailed investigation of the phenomena of hybridisation in Algae.

Polymorphism. It has already been mentioned that at the present day the ideas as to widespread polymorphism, which were beginning to be abandoned when the first edition of this work was published, are no longer entertained. A consideration of the older unsupported views is therefore no longer necessary, but it should be realised nevertheless that the majority of the freshwater Algae show considerable plasticity, especially under diverse cultural conditions[4]. While this fact in itself is of considerable importance, it is only in relatively few cases that the diversity of forms appearing in such cultures is known to exist

[1] For a detailed consideration of alternation in Algae, cf. Bonnet, Progr. Rei Bot. v, 1917, p. 1; see also Fritsch, New Phytol. xv, 1916, p. 233.

[2] cf. Andrews, Bull. Torrey Bot. Club, xxxviii, 1911, p. 299; Transeau, Amer. Nat. liii, 1919, p. 109.

[3] Pascher, loc. cit. p. 228; see also Crow, Journ. of Genetics, xiv, 1924, p. 115.

[4] cf. especially Chodat, 1913.

also under natural conditions. Few attempts have been made to follow up the facts gleaned from experiments with cultures in the laboratory by a study of the species in question in their natural environment. From the little that is known it seems probable that the degree of polymorphism exhibited in cultures is not usually realised in nature.

Numerous established cases of polymorphism are mentioned in the special portion of this book. As examples may be mentioned the *Palmella*-stages, observed in unicellular and multicellular members of different classes; the "*Tetraëdron*-stages" recorded in various Chlorococcales; the occurrence of filamentous and thalloid phases in the life-cycle of species of *Prasiola* (fig. 61); the "*Chantransia*-stages" of *Batrachospermum* and *Lemanea*, etc. Such cases are often highly instructive and useful in elucidating the affinities of the Algae in question.

CLASS I. ISOKONTAE

Within the limits here adopted, the Isokontae correspond to the old group Chlorophyceae (Green Algae) shorn of the genera and species that have been gradually transferred to the class Heterokontae (p. 295) or Yellow-green Algae, established by Luther in 1899. Saving Wille (1909, p. 2) there has been no dissentient of authority to this separation, and there can be little doubt that the Isokontae and Heterokontae represent well-marked evolutionary lines which are probably not even closely related to one another.

The Isokontae comprise a very large number of very diverse forms which enjoy a wide distribution in freshwater and terrestrial habitats, but, with a few striking exceptions, are rare in the sea. The number of species exceeds the combined total of freshwater species of all the other algal classes. In conformity with the doctrine of a flagellate evolution, the essential characteristics of the class are to be found in the features of the motile stages, but many of the distinctive peculiarities are equally recognisable in the sedentary phases, and even groups in which motility is altogether lacking (e.g. Conjugatae) show a clear Isokontan stamp. These distinctive features are: (*a*) a pigmentation of the chromatophores apparently identical with that found in the higher plants, the two chlorophylls being accompanied by only relatively small amounts of the yellow pigments; (*b*) the usual presence of pyrenoids in the chloroplasts; (*c*) the customary production of starch as a food-reserve and its frequent accumulation near the pyrenoids; (*d*) the possession of cell-walls in which cellulose is usually a clearly recognisable ingredient; and (*e*) the presence in the motile phases of equal-sized and equally orientated cilia, usually borne at the end directed forwards during movement and commonly two or four in number. Reference to the figures and descriptions of *Chlamydomonas* (p. 70) and *Ulothrix* (p. 152) will bring out plainly most of these points.

In no other class of the Algae do we find such a striking and diverse development of those types of plant-body that must be regarded as primitive and that probably illustrate something of the innumerable attempts at the production of a soma that characterised the earlier phases of the evolution of plants. This diversity has particular interest, since the Isokontae, in the pigmentation of their chromatophores and the course of photo-

synthesis, stand nearer to the main lines of evolution of the higher plants than any of the other algal classes. In contrast with the great range of simple forms it is noticeable that the Isokontae have not attained to any high degree of somatic development and, in this respect for instance, fall far short of the differentiation reached by the marine Phaeophyceae and Rhodophyceae.

A large body of forms (Chlamydomonadales)[1], well exemplified by the familiar *Chlamydomonas* (fig. 5, H, I), are characterised by normally existing as free-moving unicells, for which the motionless condition is only a passing phase in the life-cycle. Such forms differ essentially from the zoospores of sedentary types only in the usual possession of cell-walls and the prolonged retention of the capacity for movement. A few of them are naked "flagellate" forms (cf. *Pyramimonas*, p. 69, and fig. 4, C), but the vast majority of the Isokontae are of "algal" organisation, and the class does not include quite such simple types as do the Heterokontae or Chrysophyceae.

A second large series of forms (Chlorococcales) comprises those in which the dominant condition is that of a motionless unicell, which either still reverts to motility in connection with reproduction (*Chlorococcum*) or has completely lost the capacity for forming swarmers (*Chlorella* (fig. 23, A, B)). Both here and among the motile forms colonial developments are frequent. These have resulted, among Chlamydomonadales, in the production of such striking types as *Pandorina* (fig. 8) and *Volvox* (fig. 12), in which all the cells have cilia and all contribute equally to the movement of the colony. Among Chlorococcales there exist a host of diverse forms in which almost every possible type of colony would seem to be realised (cf. *Pediastrum* (fig. 28), *Dictyosphaerium* (fig. 44), *Coelastrum* (fig. 49), etc.).

Many of the colonial types among Isokontae are distinguished by a certain degree of individuality finding expression in the fact that the number of cells composing the colony is practically a constant (often some multiple of four) and is fixed in the early stages of development, no cell-division occurring after the embryonic phase, until the time arrives for the production of a new generation. Such definitely integrated colonies are spoken of as *coenobia* and are manifestly not far removed from individuals. In *Pleodorina* (fig. 10, A) and *Volvox* (fig. 12), the coenobia even exhibit division of labour among the cells, only some of which are employed for reproductive purposes. It is not improbable

[1] It is advisable to read the matter on pp. 25–30 before proceeding with the following. The general account of the Isokontae is brief, in view of the detailed consideration of the different groups.

that some of the coenobial Chlorococcales may have originated direct from free-moving coenobial forms, and neither in this respect nor in the evolution of the unicellular types of the former, is it at all necessary to assume a monophyletic origin from primitive motile types.

A less specialised kind of colony is afforded by the palmelloid members (Tetrasporales) of the Isokontae, which by way of the *Palmella*-stages (p. 65) of *Chlamydomonas*, etc., are so closely linked up with the Chlamydomonadales, that they are best placed with the latter in a common group, the Volvocales. In this may also be included the dendroid Chlorodendrales (p. 66).

Volvocales and Chlorococcales, apart from possessing the characters typical of Isokontae, also agree in the complete absence of vegetative division (cf. p. 28). Cell-formation in them is a process of rejuvenescence of the protoplast and is always closely linked up with reproduction. As long as vegetative division is lacking, however, the potentialities of the organism are distinctly limited. It was the development of the capacity for septation that led to the evolution of the higher filamentous forms and so of the higher plants. In such vegetative division the daughter-cells become separated by a septum which is common to both and for the rest they remain enveloped by the membrane of the parent. Only one member of Chlorococcales, in which this mode of division occurs, has become known, viz. *Chlorosphaera* (cf. p. 107), and that is very possibly a reduced filamentous form. The segmentation of the zoospores of *Ulothrix*, *Stigeoclonium*, etc., after coming to rest, however, fully illustrates the effect of this method of division in a unicellular individual. According as it takes place repeatedly in the same plane or in more than one plane, we obtain a filament (*Ulothrix*) or a cellular expanse (*Ulva*).

It can scarcely be questioned that the filamentous Isokontae have originated in this way from unicellular types by the inception of vegetative division[1], and again their origin is doubtless polyphyletic, even perhaps as regards the forms included in one and the same group in the following treatment. The formation of reproductive cells (zoospores, gametes, etc.) in all the filamentous types is, however, invariably accomplished by rejuvenescence of the protoplast.

It is unnecessary to trace out at this point all the varied developments of the filamentous habit among Isokontae. The forms in question are classed in the five groups Ulotrichales, Chaeto-

[1] Church (Oxford Bot. Mem. No. 3, 1919, p. 8) regards the freshwater Isokontae as highly reduced forms, but for this view there is not the slightest evidence (cf. Fritsch, New Phytol. xx, 1921, p. 166 et seq.).

phorales, Oedogoniales, Conjugatae, and Siphonales, of which the last represents a very distinct line characterised by lack of septation in the vegetative phase (e.g. *Vaucheria*). Elaboration of the simple filament has been attained in several groups by branching and in some cases (*Cladophora* (fig. 64), *Draparnaldia* (fig. 70)) this is accompanied by differentiation of more or less specialised main axes. The most highly evolved morphological type among Isokontae is found in the Chaetophorales, where many genera (cf. *Stigeoclonium* (fig. 2, II), *Trentepohlia*) exhibit a differentiation of the thallus into a prostrate and a projecting system, a type of construction which finds its parallel in the simpler filamentous members of Phaeophyceae and Rhodophyceae (cf. *Chantransia*). By more or less complete reduction of the projecting system purely prostrate epiphytes (*Aphanochaete* (fig. 67), etc.) or even discoid types (*Coleochaete* (fig. 81)) result.

The majority of the filamentous Isokontae (except *Sphaeroplea* and some Zygnemaceae) in young stages possess a special basal attaching cell, usually with scanty chlorophyll and more or less numerous lobes which flatten out against the substratum (fig. 87, A); this *hapteron* mostly originates from the colourless anterior end of the zoospore. As the threads lengthen, however, they usually break away from their attachment and thereafter float freely. This is but the first step in the prolific vegetative reproduction by fragmentation that occurs in most of the filamentous forms (esp. Zygnemaceae), whereby the extensive floating tangles to which they owe the name of "pond-scums" are produced. Growth is usually intercalary, but in a few cases (e.g. *Cladophora*) there is a definite apical cell. The Oedogoniales are distinguished by a very specialised method of cell-division (cf. p. 214).

In view of the immense range of form within the Isokontae, the cell-structure naturally exhibits considerable diversity. The cell-membrane, when thickened, frequently shows pronounced stratification (especially evident after treatment with strong acids); in the main it seems to consist of cellulose (blue with chlor-zinc-iodide), but in many of the filamentous forms an outermost layer, frequently spoken of as the "cuticle" and often appearing quite sharply defined, is chemically different. External to the actual membrane there are frequently present gelatinous pectose layers (not coloured by chlor-zinc-iodide), which exhibit all stages between insolubility and complete solubility in water and which often appear to be continuously exuded. The resulting envelopes of mucilage[1] are best seen in many

[1] cf. especially Klebs, Unters. Bot. Inst. Tübingen, II, 1886, p. 333; Schröder, Verhandl. Nat.-Med. Ver. Heidelberg, VII, 1902, p. 139.

Chlorococcales (fig. 43) and Conjugatae. Such envelopes are strikingly lacking in *Vaucheria* and Cladophoraceae which as a consequence provide a home for a rich epiphytic flora, unable to settle on a mucilaginous substratum. Mucilage-envelopes usually stain readily with aniline dyes, such as fuchsin, safranin, methyl blue, and gentian violet, and also become obvious on mounting material in a drop of water to which sepia has been added. The mode of origin of the mucilage-envelopes is in many cases by no means clear, but in the Desmids there are evident pores (fig. 102, C) in the cell-walls through which the mucus is excreted, whilst in certain other cases it appears to arise by gelatinisation of cell-membranes.

The chloroplasts[1] are well defined except in a few cases (older cells of *Hydrodictyon*, *Sphaerella*, *Characium Sieboldii*) and, apart from outward habit, form the chief basis for generic distinction. Very often there is only one chloroplast in the cell, as in nearly all Volvocales, Chlorococcales, and many of the filamentous forms. The type of cell prevalent among higher plants, with many small discoid chloroplasts, is exceptionally rare among Isokontae, though found in *Eremosphaera* (fig. 31) and in the Siphonales. Very elaborate types of chloroplast are encountered in the Conjugatae, where there are usually two or more per cell. In most cases the chloroplasts lie in the lining layer of cytoplasm (i.e. are parietal), but central or axile chloroplasts are not uncommon (cf. *Asterococcus*, *Trebouxia* (fig. 23, K), *Prasiola* (fig. 61), many Desmids). Elaboration of the chloroplasts is often apparently related to increase in the size of the cells.

In the vast majority of the Isokontae the chloroplasts contain *pyrenoids*[2], although these are regularly lacking in certain cases (e.g. *Microspora*, *Vaucheria*). Such pyrenoids consist of a central protein-body or "pyreno-crystal," often rounded but sometimes angular, surrounded by a very characteristic envelope of small, closely apposed starch-grains which in rare cases appear to be confluent; this "starch-sheath" is often separated by a slight gap from the pyreno-crystal and in some Desmids is several-layered. Starch-accumulation is usually not confined to the neighbourhood of the pyrenoids, abundant mostly larger starch-grains being deposited during active photosynthesis in the general stroma of the chloroplast. In *Hydrodictyon* according

[1] The detailed literature is cited under the individual genera. An excellent general treatise was published by Schmitz (1882), but there have been many emendations.

[2] Boubier, Bull. Herb. Boissier, VII, 1899, p. 451; Bourquin, Bot. Gaz. LXIV, 1917, p. 426.

to Timberlake[1] and *Cladophora* according to Carter[2], however, all the starch is derived from the pyrenoids. The starch-sheath of the pyrenoids possesses a greater degree of permanency than the stroma-starch, which is always removed first under conditions of starvation.

The pyreno-crystal represents a store of reserve-protein, but the exact conditions that bring about the utilisation of this reserve are not yet adequately established. Starvation frequently causes a disappearance of pyrenoids, whilst, if cells are well nourished, they often increase in number. The pyreno-crystal may thus perhaps be compared with the protein crystalloids that are not rarely encountered in the chloroplasts of higher plants, but the pyrenoids of most Isokontae seem to possess a strange degree of individuality that differentiates them from a mere food-reserve. Thus, in some forms possessing but one pyrenoid in the chloroplast (e.g. *Pyramimonas*[3]) the pyrenoid divides when division of the protoplast takes place. They also multiply without the occurrence of cell-division (e.g. in the chloroplasts of *Spirogyra*). On the other hand in many cases they seemingly disappear completely during cell-division, apparently arising *de novo* in the daughter-cells[4]. In a number of forms (e.g. *Ankistrodesmus falcatus* (Corda) Ralfs, *Debarya calospora* (Palla) W. & G. S. West) they may be present or absent according to circumstances.

The majority of the Isokontae have uninucleate cells, but a multinucleate condition is seen in Cladophoraceae and, probably as a preparation for the formation of reproductive elements (zoospores, gametes), in several Chlorococcales such as *Chlorococcum* and *Hydrodictyon*. A multinucleate condition also obtains throughout the Siphonales which can be regarded as unseptate multicellular individuals. In many cases the nucleus seems to differ but little in structure from that of higher plants, but there is frequently a scanty chromatin network, the bulk of the chromatin being lodged in the nucleolus or rather in its peripheral part. Such nuclei, and those of the ordinary type may, however, occur side by side within the same group.

The methods of reproduction are naturally very diverse. Vegetative multiplication is of widespread occurrence and consists in the disrupture of the body into two or more pieces (e.g. *Dictyosphaerium*, many filamentous forms). Multiplication

[1] Ann. of Bot. xv, 1901, p. 624.
[2] Ibid. xxxiii, 1919, p. 475.
[3] Dill, Jahrb. Wiss. Bot. xxviii, 1895, p. 344.
[4] cf. for instance Smith, Ann. of Bot. xxxii, 1918, p. 462; Hodgetts, New Phytol. xv, 1916, p. 114; Grove, New Phytol. xiv, 1915, p. 173.

by ordinary (vegetative) cell-division is characteristic of *Pleurococcus* and Desmids.

Asexual reproduction by zoospores is exceedingly abundant among the members of the class and affords a means by which rapid dispersal throughout a piece of water is effected. Zoospores are lacking in the whole group of the Conjugatae, as well as in the autosporic Chlorococcales. In the unicellular Chlamydomonadales the daughter-individuals produced by division of the protoplast of the parent are comparable to the zoospores of the sedentary Chlorococcales, Ulotrichales, etc., whilst in the coenobial forms among Chlamydomonadales and in the Hydrodictyaceae the daughter-coenobia may be regarded as produced from zoospores which have failed to become independent (cf. also the synzoospores of *Vaucheria*, p. 290). The zoospores are invariably naked and formed from the protoplast only of the parent-cells, the latter producing either a single (Oedogoniales) or several swarmers. Specialised sporangia are rarely developed, but are seen for example in *Trentepohlia* (fig. 80). The zoospore itself is most commonly spherical or pear-shaped and possessed of a more or less marked colourless beak at the anterior end from which two or four cilia arise; in the Oedogoniales, however, there are numerous cilia forming a fringe at the base of the beak (fig. 88).

Aplanospores (p. 43) are of frequent occurrence, both in forms normally producing zoospores (e.g. *Chlorococcum*, *Ulothrix*) and as a permanent development in many genera obviously derivable from zoosporic types (e.g. *Chlorella* and allied Chlorococcales). Akinetes are also commonly encountered (*Ulothrix*, *Microspora*, etc.).

Sexual reproduction is known in most of the families of Isokontae, but is completely lacking in the autosporic Chlorococcales. With the exception of the Chlorococcales and the purely oogamous Oedogoniales, it is possible in each group to distinguish both isogamous forms and others showing a more or less marked degree of anisogamy, often amounting to oogamy; in the Siphonales however the isogamous forms are marine. Oogamy has been attained by certain Chlamydomonadales, *Cylindrocapsa*, *Sphaeroplea*, *Coleochaete*, Oedogoniales, and *Vaucheria*. In general the oogamous representatives of the filamentous series occupy a peculiarly isolated position and are not easily related to the other members of their groups.

Apart from the Conjugatae, which exhibit a method of sexual reproduction peculiar to themselves, the gametes or at least the spermatozoids are motile. In the isogamous and anisogamous types sexual fusion occurs outside the parent, whilst the stationary ovum of the oogamous types is invariably fertilised *in situ*.

The product of sexual fusion is almost invariably a thick-walled resting zygospore or oospore which sinks to the bottom of the water and, if the latter dries up, may be dispersed by the wind. The germination of these sexually produced resting-stages has been observed only in relatively few cases. It would seem that the first two divisions bring about reduction to the haploid number of chromosomes and not uncommonly lead to the formation of four individuals (Oedogoniales, *Ulothrix*, Mesotaeniales), although there may be only two or one. *Coleochaete* is the only member of Isokontae in which the zygote divides to form a multicellular structure which produces swarmers giving rise to the ordinary thallus. This apparent sporophyte is however haploid, since reduction occurs with the first division of the zygote nucleus.

The Isokontae play a very important rôle in the subaerial and freshwater vegetation of the world. Such genera as *Pleurococcus* (*Protococcus*), *Prasiola*, *Hormidium*, etc., are common members of the terrestrial flora, whilst *Zygogonium ericetorum* covers acres of peaty and sandy soil in temperate regions. Many Isokontae are also known to occur in the subterranean soil-flora, although we have no data as to their abundance.

Members of this class are found in most kinds of waters, although few are known from hot springs. Whilst some are practically ubiquitous, others are restricted to very definite habitats, many examples of which are mentioned in the following under the individual genera. A large number of the Isokontae occur in the freshwater plankton and many of the Chlorococcales (p. 100) and Desmids are very highly adapted to such a free-floating existence. A certain number are common epiphytes on larger Algae and other aquatics (e.g. *Characium*, *Aphanochaete*, *Bulbochaete*, etc.), a few are endophytes (cf. *Chlorochytrium*, *Phyllobium*, *Endoderma*), whilst a limited number have become parasitic[1].

The Isokontae in this work are classified in seven groups which may be briefly characterised as follows:

I. *Volvocales*. Unicellular or colonial, either motile throughout life (Chlamydomonadales) or forming sedentary colonies of

[1] *Phyllosiphon Arisari* Kühn (a member of Siphonales, see Bot. Zeit. XXXVII, 1879, p. 322; and Maire, Bull. Soc. Bot. France, LV, 1908, p. 162) is parasitic on the leaves of *Arisarum vulgare* and occasionally of *Arum maculatum* in Italy and the south of France, causing yellow spots, whilst other species of the genus have been recorded as parasites on the leaves of various plants in Ecuador (cf. Lagerheim, Nuova Notarisia, III, 1892, p. 120). *Cephaleuros* (Trentepohliaceae) is parasitic on the leaves of various tropical plants, including Tea (*Thea sinensis*), causing a serious disease of the latter (Mann and Hutchinson, Mem. Dep. Agric. India, I, 1907, Bot. Ser., No. 6).

a palmelloid (Tetrasporales) or dendroid (Chlorodendrales) type, the individuals of which readily revert to a motile condition. Almost exclusively freshwater.

II. *Chlorococcales.* Unicellular or colonial, motionless in the ordinary vegetative condition and either reproducing by zoospores (Zoosporinae) or by aplanospores (Autosporinae). Almost exclusively freshwater.

III. *Ulotrichales.* Filamentous, the plant-body consisting of a simple unbranched filament or cellular expanse with small cells and a parietal (Eu-ulotrichales) or an axile stellate (Prasiolales) chloroplast; or of a simple or often branched filament with large multinucleate cells and elaborate chloroplasts and either isogamous (Cladophorales) or oogamous (Sphaeropleales). A certain number marine.

IV. *Chaetophorales.* Filamentous, plant-body often sharply differentiated into a prostrate and a projecting system, though the latter is often reduced and the former in some cases pseudoparenchymatous and discoid; in many genera hairs are developed, though this is not an invariable rule. Most genera isogamous. Mostly freshwater.

V. *Oedogoniales.* Filamentous, filaments simple or branched, zoospores multiciliate, oogamous; division of cells characterised by intercalation of strips of membrane between the mother-cell and the distal end of the daughter-cell. Exclusively freshwater.

VI. *Conjugatae* Unicellular, colonial, or filamentous, usually with elaborate chloroplasts. No motile stages. Reproduction by cell-division and by conjugation. Exclusively freshwater.

VII. *Siphonales.* Filamentous, threads without septa, coenocytic. Mostly marine, the only freshwater forms oogamous.

There is little difficulty in discriminating between the five filamentous groups, or between the main bulk of the Volvocales and Chlorococcales. In a few genera of the latter group, however, in which abundant mucilage-production occurs, the mature colonies may come to resemble those of some Tetrasporales, and one may occasionally be in doubt about the assignation of a given form. Attention must also be paid to the cell-features, otherwise confusion with parallel forms belonging to other classes is likely to occur (cf. p. 33).

GROUP 1. VOLVOCALES

The normally motile members of the Isokontae, with their manifold modifications, are conveniently grouped together as Chlamydomonadales, the series taking its name from the important genus *Chlamydomonas* which constitutes a central type.

The numerous forms belonging to this series are relatively well known through the work of Dangeard, Dill, Goroschankin, Chodat, Wille, Kofoid, Shaw, and G. S. West. They sometimes occur in prodigious quantity in stagnant water, giving it a pale green colour and a somewhat unpleasant odour, and are occasionally the cause of foulness of drinking water, imparting to it a distinctly oily taste[1]. According to Griffiths (1923, p. 208) they are associated with good aeration of the water, either through the photosynthetic processes of an abundance of macrophytic vegetation or through the inflow of aerated water; they are well represented in the plankton of the slower-flowing rivers. Some of the unicellular forms occur in brackish water (West, 1915, p. 73) and others are found in the soil (Bristol, 1920; Jacobsen[2]).

The ordinary individual (figs. 4, 5, 11) is actively motile by means of two cilia (four in *Pyramimonas* and *Carteria* (cf. fig. 5, A)) which are generally directed forwards during movement, although in *Scourfieldia* (fig. 6, D, E) the cell moves with its posterior end foremost. In most cases the forward motion is accompanied by a rapid rotation of the organism upon its longitudinal axis. The cells invariably contain a single chloroplast which, in the Chlamydomonadaceae, usually takes the form of a cup or bell open towards the anterior end and often strongly thickened in the posterior region where a median pyrenoid is commonly situated (fig. 5, II, I); the latter may however be absent or be differently located (*Brachiomonas*, *Lobomonas*). At the front-end the chloroplast thins out, so that the anterior part of the protoplast is colourless. Here the membrane is often thickened to form a more or less prominent beak on either side of which the two cilia arise, whilst the two contractile vacuoles (fig. 5, II, *cv*) characteristic of this type of cell are situated just beneath the points of insertion of the latter. The nucleus is usually suspended in the hollow of the chloroplast. The structure just described is typical of many members of the Volvocales and may be briefly referred to in the subsequent matter as the Chlamydomonad type.

In the Sphaerellaceae (fig. 11), however, the chloroplast is less sharply defined, being a more or less reticulate structure occupying most of the periphery of the protoplast and containing a number of scattered pyrenoids. The cell-wall moreover is strongly thickened and gelatinous and is usually traversed by simple or branched processes extending from the protoplast up to the firmer bounding layer of the membrane. There are numerous contractile vacuoles in the peripheral protoplasm. The differences

[1] Whipple, Trans. Amer. Micr. Soc. xxi, 1900, p. 97.
[2] Jacobsen, Zeitschr. f. Bot. ii, 1910, p. 145.

of cell-structure between Chlamydomonadaceae and Sphaerellaceae are sufficiently striking to warrant the assumption that they represent distinct evolutionary lines from the Isokontan ancestry. An eye-spot, variable both in form and position, but always in contact with the chloroplast, is present in both types of cell.

A certain number of unicellular Chlamydomonadales possessing the Chlamydomonad type of organisation are characterised by lacking a cell-wall, with an accompanying power of slight alteration of the shape of the protoplast. Some of these, grouped as Polyblepharidaceae (*Pyramimonas* (fig. 4, C), *Polyblepharis*), are perhaps primitively naked and transitional between the unknown flagellate ancestors and the algal members of the Isokontae. Support for this view is furnished by the absence of sexuality, by the fact that division is always longitudinal (fig. 4, D), and that cysts are readily formed[1]. In the case of *Dunaliella* (fig. 6, F), however, where a sexual process has been observed and the cell-structure is very similar to that of a *Chlamydomonas*, Pascher[2] is probably right in regarding the naked character as secondary. *Polytoma* (fig. 4, F) is a colourless Chlamydomonad which has lost its chloroplast, although still producing starch.

A peculiar, and probably not natural, family is constituted by the Phacotaceae, where the cell is surrounded by a thick, often specially differentiated envelope, closely enshrouding the protoplast (*Pteromonas* (fig. 13, D–H)) or separated from it by a space (*Phacotus* (fig. 13, B–C), *Coccomonas* (fig. 13, M)); in some cases at least there is a distinct cell-wall apart from the envelope (*Coccomonas*). The details of cell-structure are imperfectly known, but the chloroplast would appear to be of the Chlamydomonad type, with one or sometimes several pyrenoids. Two of the genera (*Phacotus*, *Pteromonas*) show a marked compression of the cell, a condition also seen among Chlamydomonadaceae in *Scourfieldia* (fig. 6, D, E).

The commonest method of reproduction among these unicellular forms is an asexual one, the individuals either remaining motile (*Brachiomonas* (fig. 6, J), *Sphaerella*, *Pyramimonas*) or withdrawing their cilia and coming to rest (*Chlamydomonas*, *Phacotus*). Where the organism is possessed of an envelope, the process is initiated by a slight contraction of the protoplast which thereupon undergoes constriction along successive planes at right angles to one another[3] to form usually four or eight

[1] cf. Dill, Jahrb. Wiss. Bot. XXVIII, 1895, p. 342.
[2] Pascher, Hedwigia, LII, 1912, p. 283.
[3] The first division-plane is longitudinal in some species, apparently

daughter-individuals. These generally acquire all the characteristics of the parent (the distinctive shape in *Brachiomonas* (fig. 6, J), the peculiar bivalved envelope in *Phacotus* (fig. 13, A), etc.) before they are set free by the rupture of its membrane. In *Pyramimonas* (fig. 4, D) the number of cilia gradually increases during division, whilst in *Dunaliella* (fig. 6, G) each daughter-individual receives one cilium from the parent and forms the other *de novo*[1].

The sexual process in the forms under consideration is almost invariably isogamous, the only marked exceptions being afforded by *Chlamydomonas coccifera* Gorosch. and *C. monadina* Stein; slight differences in the size of the gametes have however been noted in *Brachiomonas*, *Dunaliella*, and *Chlorogonium*. A sexual process is unknown in the Polyblepharidaceae and has not so far been recorded in all the other genera. The production of gametes takes place in the same way as in the asexual multiplication of individuals, but division usually goes further and the resulting swarmers are smaller. The gametes are naked (fig. 5, D, E), except in a few species of *Chlamydomonas* (e.g. *C. media* Klebs) and in *Lobomonas*, where they are provided with a delicate membrane, marking a very primitive condition. In these cases the gametes either slip out of their membranes just prior to fusion or they meet by their anterior ends and a kind of conjugation-canal is established within which fusion occurs[2]. This is also the case in *C. monadina*, where however there is a sharp differentiation into large relatively inactive macrogametes (female) and small actively motile microgametes (male, cf. fig. 3, E, F); in *C. coccifera* the macrogamete loses its cilia prior to fusion[3]. The zygote frequently continues movement for a short time, but sooner or later rounds off to form a thick-walled zygospore, often with reddish contents harbouring an abundance of oil.

Encystment of the protoplast, frequently subsequent to escape from the cell-membrane, has been observed in *Chlamy-*

transverse in others; in still other cases (*Chlamydomonas longistigma* Dill, etc.) division commences in the longitudinal plane, but before constriction is complete the protoplast gradually rotates through 90°, so that the process concludes in the transverse plane (cf. Dill, loc. cit. p. 330). Where the matter has been fully investigated, it appears that a similar rotation occurs also in those species in which division is apparently transverse (cf. Dangeard, Le Botaniste, VIII, 1901, p. 25).

[1] The *Palmella*-stages found in certain Chlamydomonadaceae are considered on p. 65.

[2] cf. Klebs, 1896, p. 429; Dill, loc. cit. p. 332.

[3] cf. Goroschankin, Bull. Soc. imp. Nat. Moscou, 1890, p. 507; and Flora, XCIV, 1905, p. 420.

domonas gigantea Dill and is very common in *Sphaerella* (cf. p. 79); as above mentioned it also occurs in *Pyramimonas*.

The colonial members of the Chlamydomonadales all form coenobia (cf. p. 52) composed of a definite number of cells. It appears that this habit has originated separately in Chlamydomonadaceae and Sphaerellaceae[1] and in both families has culminated in the development of a hollow sphere, beyond which further progress is impossible. In either case the simpler forms

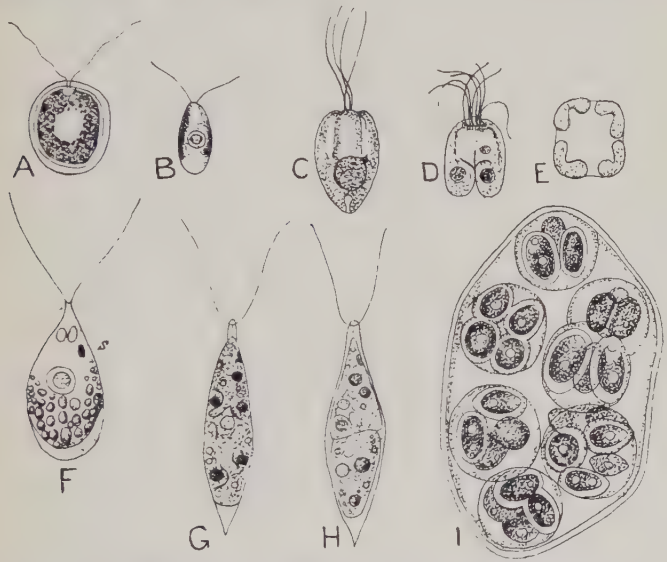

Fig. 4. A, *Chlamydomonas globulosa* Perty (after West, ×345), from Earlswood, Warwickshire. B, *C. elegans* G. S. West (after West, ×345), from Sutton Park, Warwickshire. C–E, *Pyramimonas delicatulus* Griff. (after Griffiths, ×600), from Stanklin Pool, Kidderminster; D, dividing individual; E, anterior view. F, *Polytoma uvella* Ehbg. (after Francé, ×500). G–H, *Chlorogonium euchlorum* Ehbg. (after Jacobsen, ×645); H, dividing individual. I, *Chlamydomonas monadina* Stein, *Palmella*-stage (after Goroschankin, ×590). *s*, eye-spot.

exhibit arrangement of the cells in one plane (*Gonium* (fig. 7, A), *Stephanosphaera*), a production of daughter coenobia from each cell of the parent, and an isogamous sexual process.

Among the Chlamydomonadaceae a very complete series is found showing a gradual increase in the number of cells and the size of the coenobium, and this is accompanied by a differentiation of reproductive from vegetative cells and a replacement of isogamy by oogamy; but the highest type of all is attained by

[1] cf. Crow, New Phytol. xvii, 1918, p. 151 et seq.

Volvox among the Sphaerellaceae (fig. 12). The mature coenobium in all these forms is more or less spherical or ellipsoidal, but in the early stages of its development it appears as a flat or slightly curved plate (plakea) which, by gradual involution during further cell-division, closes in to form a sphere. The last point on the sphere to close (phialopore) becomes the posterior end (aboral pole) of the new coenobium[1]. In *Pandorina* (fig. 8, A) a more or less solid coenobium is produced by subsequent growth of the cells towards the centre, but in the other forms the sphere remains hollow (*Eudorina* (fig. 9, A), *Pleodorina* (fig. 10, A), *Volvox* (fig. 12)). Movement is effected by the combined action of the cilia of all the constituent cells and, as already indicated, one point on the sphere opposite the phialopore is always directed forwards; at the same time the coenobium rotates on its axis. As a general rule the cells in the anterior half have appreciably larger eye-spots. All the colonial forms so far mentioned have biciliate cells, but in *Spondylomorum* they are quadriciliate, as in *Carteria*.

In *Pandorina* and *Eudorina* daughter-coenobia are formed from the divided protoplasts of all the cells of the parent (cf. fig. 8, B), but in *Pleodorina* and *Volvox* only certain cells (often called *gonidia*), which sooner or later become distinguishable by their larger size, fulfil a reproductive function, the remainder being purely vegetative; here therefore part of the parent ultimately dies away as the penalty of the greater specialisation. In *Pleodorina illinoiensis* Kofoid (fig. 10, A) all but four of the cells at the anterior end act as gonidia, but in *P. californica* Kofoid only those of the posterior half are reproductive. In *Volvox*, where the coenobia comprise several thousand cells, only a very small number (1–25) are set aside as gonidia; the latter are again located in the posterior half, but are separated from one another by tracts of vegetative cells and betray their greater specialisation by losing their cilia at an early stage. There are considerable differences among the species of *Volvox* in the time of differentiation of the gonidia and the details of formation of the daughter-coenobia, features which have been carefully studied by W. R. Shaw and used by him as a basis for dividing up *Volvox* into a number of genera (cf. p. 81).

The sexual process in these forms shows many points of interest. In *Pandorina* (fig. 8, C–H), where it has been only

[1] For details see especially Merton, Zeitschr. f. wiss. Zool. xc, 1908, p. 464; Conrad, Rec. Inst. bot. Bruxelles, ix, 1913, p. 334; Grove, New Phytol. xiv, 1915, p. 173; Janet, Le Volvox, Limoges, 1912; Harper, Mem. Brooklyn Bot. Gard. i, 1918, p. 154; Hartmann, Archiv f. Protistenk. xlix, 1924, p. 375.

rarely observed, the fusing gametes are often somewhat different in size and behaviour, but in the other genera there is more or less pronounced oogamy. The coenobia are usually dioecious, although *Eudorina* is sometimes monoecious and so are several species of *Volvox* (cf. fig. 12, A). In *Eudorina* and *Pleodorina* every cell or nearly all the cells of the female coenobia constitute ova, whilst in the male each cell becomes an antheridium, developing by division of its protoplast a bundle of elongated, pale greenish or yellowish, biciliate spermatozoids[1] (fig. 9, E, F). In *Volvox* matters are much the same, but only a limited number of cells develop as ova (fig. 12, A, *g*) and antheridia (*a*) and the former in the mature condition are devoid of cilia. After liberation the spermatozoid-bundles cohere for a time and approach the female cells, whereupon the individual sperms separate and fusion occurs. Reduction is stated to take place at the first division of the oospore in the case of *Volvox*[2].

In various species of *Chlamydomonas* and *Carteria* the asexual division-process, under certain unknown conditions, is modified through the failure of the daughter-cells to develop cilia and a progressive gelatinisation of the membranes of the consecutive generations. The resulting "*Palmella*-stages" often attain to considerable dimensions and vary in appearance, according as the mucilage is diffluent or the strata formed by the successive mother-cell membranes remain distinct (fig. 4, I). In the majority of cases these stages are only observed occasionally and are probably of brief duration, but in some species (e.g. *Chlamydomonas Kleinii* Schmidle)[3] they become the dominant condition. From such forms it is only a slight step to the Algae grouped below as Tetrasporales, in which motility only occurs in connection with reproduction and the cells of the colonies are held together solely by the mucilage in which they are embedded. A certain number of these forms, in which the four division-products of a parent-cell commonly remain grouped together, and structures known as pseudocilia (cf. below) are present, appear to form a natural group, the Tetrasporaceae. But it is also convenient to include in the Tetrasporales a number of other genera lacking these precise characteristics, but in which the cells are loosely embedded in copious mucilage. It is unlikely that these Palmellaceae constitute a natural family and the possibility of some of them being reduced forms must be kept

[1] Interesting observations on sex distribution in *Gonium* and *Eudorina* have recently been made by Schreiber (Zeitschr. f. Bot. XVII, 1925, p. 348 et seq.).

[2] Zimmermann, Jahrb. wiss. Bot. LX, 1921, p. 274.

[3] Schmidle, Flora, LXXVII, 1893, p. 16.

in mind; many genera formerly placed here have now found a position elsewhere[1].

The cell-structure in all the Tetrasporales appears to resemble the Chlamydomonad type, the chloroplast being often cup-shaped and usually provided with a pyrenoid. The zoospores and isogametes—the latter observed as yet only in a few forms—are almost replicas of a *Chlamydomonas*-cell, except for the absence of a wall. The reproduction of most of the forms involved is however imperfectly known and would appear to vary considerably with the conditions of the environment, a very frequent phenomenon in lowly algal types. Thus, the zoospores of *Tetraspora*, on coming to rest, are stated either to divide with copious mucilage-formation to form a colony of the normal type, or to give rise to thick-walled resting spores with reddish contents, or to develop *Palmella*-stages of indefinite shape.

The *pseudocilia* of the Tetrasporaceae are fine protoplasmic threads extending from the outer end of the cell to the surface of the enveloping mucilage (fig. 21, B); in *Apiocystis* (fig. 22) they even extend beyond the latter, the projecting portions being provided with special mucilage-sheaths of their own[2]. As a rule they are not readily seen before the application of appropriate stains (safranin, gentian violet) and are often very difficult to recognise. They vary in number from two to four in *Tetraspora* (fig. 21, B) to many in *Schizochlamys* (fig. 21, D). Functionally they have nothing to do with cilia, from which they also differ in length and other features; when swarmers are produced the pseudocilia are discarded. They may have a respiratory function, a view which receives some little support from their projection in *Apiocystis*, where the surface-mucilage is especially firm.

A third line of development among the Volvocales has resulted in branched dendroid colonies (fig. 2, D), parallel with analogous forms found in other groups (cf. *Mischococcus*, *Colacium*). The colonies are produced in various ways, commonly by a one-sided secretion of mucilage (*Hormotila* (fig. 14)). Since the cells in many of these forms have a Chlamydomonad structure, a reference to the Volvocales is plainly indicated. The change on the part of the sedentary cells to the motile state is obviously accomplished with great ease and both the biciliate

[1] Thus *Mischococcus* (p. 302) has been transferred to the Heterochloridales, *Oocardium* (p. 283) to the Desmidiaceae, *Dictyosphaerium* (p. 134) to the Chlorococcales, *Radiofilum* (p. 157) and *Hormospora* (p. 156) to Ulotrichales, etc.

[2] The projection of the pseudocilia shown for *Tetraspora lubrica* (Roth) Ag. in fig. 111, C of the first edition of this work certainly represents a very exceptional condition.

(*Hormotila*, *Chlorangium*) and quadriciliate (*Chlorodendron*, (fig. 2, D)) types are represented. Moreover eye-spots and contractile vacuoles are often recognisable, even during the sedentary phase. It is not improbable that these forms arose directly from the ancestral flagellate stock, and it is worthy of note that sexuality has so far not been observed among them. Most, however, are very incompletely known and apparently of rare occurrence[1].

Three series are thus distinguishable among the Volvocales, viz.:

I. *Chlamydomonadales*, in which the dominant phase in the life-cycle is a motile one, the different genera being either unicellular or coenobial.

II. *Chlorodendrales*, in which the dominant phase is a sedentary one, the individuals being united to form dendroid colonies.

III. *Tetrasporales*, in which the dominant phase is again sedentary, the individuals being embedded in mucilage to form colonies with or without definite shape.

The following scheme should aid in the identification of the British genera of the group:

Series I. *Chlamydomonadales*.

A. Unicellular, naked, chloroplast cup-shaped, lobed at the front end, four cilia — *Pyramimonas* (*Polyblepharidaceae*)

B. Unicellular or coenobial, cell-wall usually rather thin (cf. also *Chlorogonium* under C), chloroplast typically cup-shaped with one or more pyrenoids usually located at the back end, two or four cilia — *Chlamydomonadaceae*

a. Individuals biciliate — *Chlamydomonadeae*

1. Unicellular.

* Chloroplast present.

† Cell-wall present.

§ Cells not compressed, cilia of moderate length.

⊙ Cells spherical, ovoid, or ellipsoid; pyrenoid, when single, median in position and usually at posterior end — *Chlamydomonas*

⊙⊙ Cells lobed, pyrenoid posterior and somewhat lateral — *Lobomonas*

⊙⊙⊙ Cells with a number of pronounced posterior arms, chloroplast rather indefinite, pyrenoid commonly anterior and lateral — *Brachiomonas*

§§ Cells markedly compressed, cilia about four times the length of the body — *Scourfieldia*

[1] cf. Davis, Ann. of Bot. VIII, 1894, p. 377 (*Euglenopsis* Davis = *Chlorodendron* Senn); Bohlin, 1897, p. 7; Fritsch, 1918, p. 494.

†† Cell-wall lacking — *Dunaliella*
** Chloroplast absent — *Polytoma*
2. Coenobial.
† Coenobium a flat plate of 4 or 16 cells — *Gonium*
†† Coenobium a compact sphere or ellipsoid of 16 or 32 cells — *Pandorina*
††† Coenobium a hollow sphere or ellipsoid
§ Coenobium without special gonidia — *Eudorina*
§§ Coenobium with special gonidia in the posterior region — *Pleodorina*
b. Individuals quadriciliate — *Carteria* (*Carterieae*)

C. Unicellular or coenobial, cell-wall relatively thick and traversed by protoplasmic strands (except *Chlorogonium*), chloroplast not sharply defined with scattered pyrenoids, two cilia — *Sphaerellaceae*
a. Unicellular.
1. Cells fusiform, elongate, with a thin wall — *Chlorogonium*
2. Cells ovoid, with a thick wall traversed by protoplasmic strands — *Sphaerella*
b. Coenobial, of numerous cells, gonidia few — *Volvox*

D. Unicellular, with a thick envelope, separating into two or more portions (sometimes obvious in vegetative individuals) during reproduction, biciliate — *Phacotaceae*
a. Envelope of two more or less distinct valves, cells compressed
1. Envelope rugulose, calcified, separated from protoplast by a marked space — *Phacotus*
2. Envelope smooth, silicified (?), closely investing the protoplast — *Pteromonas*
b. Cells not compressed, envelope separated from protoplast by a space
1. Envelope ovoid or 4-angled, one cilial aperture, protoplast with a distinct cell-wall — *Coccomonas*
2. Envelope asymmetrical, roughly ovoid, two cilial apertures, protoplast naked — *Dysmorphococcus*

Series II. *Chlorodendrales.*

Only British genus — *Hormotila*

Series III. *Tetrasporales.*

A. Cells without pseudocilia — *Palmellaceae*
a. Cells irregularly grouped within structureless mucilage, chloroplast cup-shaped or sometimes a parietal plate
1. Cells globose
* Colony of indefinite shape — *Palmella*
** Cells grouped in a cylindrical mass of mucilage, often branched — *Palmodictyon*
*** Colony globose, free-floating — *Sphaerocystis*

2. Cells ellipsoid — *Coccomyxa*
3. Cells spindle-shaped — *Elakatothrix*

b. Cells grouped within a more or less stratified mucilage-envelope

1. Cells usually globose

* Chloroplast axile, star-shaped, mucilage-envelope very wide — *Asterococcus*

** Chloroplast parietal, colonies indefinite — *Gloeocystis*

2. Cells ellipsoid — *Dactylothece*

B. Cells with pseudocilia, commonly in fours — *Tetrasporaceae*

a. Cell-wall commonly rupturing into one or more pieces, persisting in the surrounding mucilage — *Schizochlamys*

b. Cell-wall not showing this character

1. Colonies of no definite shape — *Tetraspora*
2. Colonies pear-shaped, usually epiphytic — *Apiocystis*

Series I. CHLAMYDOMONADALES[1]

Family 1. POLYBLEPHARIDACEAE

The forms included here are motile Flagellates, closely related to the Chlamydomonadaceae (cf. p. 61). They are unicellular, naked, with a varying number of cilia, and the protoplast shows some power of change of shape. Reproduction is by longitudinal division, usually during movement (fig. 4, D), and resting cysts are readily produced. No sexual process has been observed. The best-known genera are *Pyramimonas* and *Polyblepharis*[2], of which only the former has so far been found in this country.

Pyramimonas Schmarda, 1850[3]. Cells pyramidal or heart-shaped, more or less lobed towards the anterior end, 4-ciliate. Chloropl. cup-shaped, often divided into four lobes in front, with a large pyren. in the thickened posterior portion: contr. vacs. and eye-spot present or absent. Reprod. by longit. div., commencing at the posterior end, during movement or of resting individuals. Resting cysts formed by rounding off of protoplast and excretion of a thick membrane.

P. delicatulus Griff. (fig. 4, C–E) is a rare form whose cells are 20–26 l.: its distinguishing features are the incisions at the ends of the chloropl. lobes (fig. 4, E) and the flask-shaped cavity at the posterior extremity of the chloropl. The only other Brit. sp. is

[1] All measurements, except where otherwise stated, are given in terms of μ (one-thousandth of a millimetre). l. = length; br. = breadth.

[2] cf. Dangeard, Ann. sci. nat., 7 sér., Bot. VII, 1888, p. 152.

[3] cf. Dill, loc. cit. p. 342; Griffiths, New Phytol. VIII, 1909, p. 131; Hodgetts, ibid. XIX, 1920, p. 254; Geitler, Archiv f. Protistenk. LII, 1925, p. 356.

P. inconstans Hodgetts (cells 8·8–15 l.), with more or less subpyramidal cells and a simple cup-shaped chloropl.

Family 2. CHLAMYDOMONADACEAE

This family includes a large number of unicellular and colonial genera, motile during the greater part of their life, the cells being provided with a cellulose wall and bearing two or four cilia. The chloroplast is typically cup-shaped, with one or more pyrenoids; eye-spots and contractile vacuoles are present. Asexual reproduction takes place by division of the protoplast (cf. p. 61) and in most cases a sexual process is known, which is isogamous in the simpler and attains to oogamy in the more advanced members. Cyst-formation occurs in a number of genera.

Sub-family 1. Chlamydomonadeae

Individuals biciliate.

Chlamydomonas Ehrenberg, 1833[1] (incl. *Chloromonas* Gobi, 1900; *Isococcus* Fritsch, 1914). Unicellular; cells spherical, ovoid, oblong-ellipsoid, or pyriform, anterior end often beaked between the two cilia; membrane often thin and closely adherent, but in some sp. thicker and in great part gelatinous. Chloropl. cup-shaped, though modified in some sp., occasionally lateral, usually with one median pyren. (pyren. sometimes lateral, sometimes several or none); contr. vacs. often in a plane at right angles to that in which the two cilia lie. Reprod. asexual and sexual; gametes generally isogamous (cf. p. 62); zygosp. spherical, smooth or asperulate. *Palmella*-stages frequent.

There are some 20 Brit. sp. of this genus, usually found in ponds, ditches, and rain-pools, but many have only so far been recorded from one or two localities. Common forms are: *C. Kleinii* Schmidle (28–32 l.; 8–12 br.) (fig. 5, J and K) with a characteristic chloropl., *C. Debaryana* Gorosch. (12–20 br.) (fig. 5, H and I), and *C. pulvisculus* Ehrenb. (*C. Ehrenbergii* Gorosch.; 14–26 br.). In *C. elegans* West (23–27 l.; 13–15 br.) (fig. 4, B) the cells are slightly more convex on one side than on the other and the chloropl. occupies only the median part of the cell. Several sp. lack pyrens., e.g. *C. reticulata* Gorosch. (34–38 l.; 30–33 br.) with a much lobed and perforated chloropl., *C. globulosa* Perty (21–28 l.; 19–26 br.) (fig. 4, A) with a mucous coat, 2–3 μ thick, outside the firm cell-wall, and the minute *C. Grovei* West (2·5–4·5 l.; 2·5–4 br.). Several pyrens. are found in *C. sphagnicola* Fritsch & Takeda[2] (15–27 l.; 9–22 br.) (fig. 1, A) with a thick

[1] cf. Goroschankin, Bull. Soc. imp. nat. Moscou, 1890, p. 498 and 1891, p. 101; Dill. loc. cit.; Dangeard, loc. cit. p. 125; Wille, 1903, p. 109 et seq.; West, 1915, p. 74; Hodgetts, loc. cit. p. 262.

[2] cf. Fritsch and Takeda, Ann. of Bot. xxx, 1916, p. 373.

gelatinous wall and a double beak, and *C. gigantea* Dill (34–38 l.; 24–28 br.) with a thin wall and a simple beak; the pyrens, in the former are parietal, in the latter near the inner face of the chloropl. *C. monadina* Stein (*C. Braunii* Gorosch.) is markedly anisogamous (see p. 62).

C. pluristigma Bristol (13–16 l.; 9·5–11 br.), with oval cells and two or three pigment spots, occurs in cultivated soils (Bristol, 1920, p. 72), as also do other sp. (Jacobsen, loc. cit.). *C. stipitata* Bachm. belongs to the genus *Characium*. *C. nivalis* Wille (*Sphaerella nivalis* Sommerf.) is one of the forms most commonly responsible for "red snow."

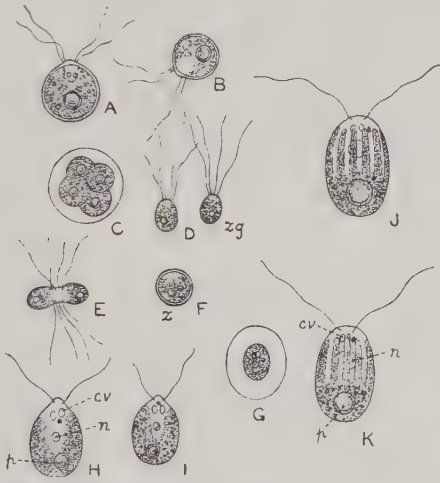

Fig. 5. A–G, *Carteria multifilis* (Fresen.) Dill, from Bradford, W. Yorks. A and B, vegetative cells; D, gametes; E, conjugating gametes; F, zygospore. H and I, *Chlamydomonas Debaryana* Gorosch., from St Just, Cornwall. J and K, *C. Kleinii* Schmidle, from Uxbridge, Middlesex. (All × 475.) *cv*, contractile vacuoles; *n*, nucleus; *p*, pyrenoid; *zg*, gamete; *z*, zygospore.

Pascher[1] has described the artificial production of hybrids between two species of *Chlamydomonas*, the offspring either resembling the two parents or affording a series of forms combining their characters in different ways.

Lobomonas Dangeard, 1899[2]. Unicellular; cells small, in general outline ovoid or angular, with a relatively thick wall provided with a number of blunt processes. Chloropl. cup-shaped, with one pyren, in a somewhat lateral position. Asex.

[1] Pascher, Ber. Deutsch. Bot. Ges. XXXIV, 1916, p. 228 and XXXVI, 1918, p. 163.

[2] Dangeard, Le Botaniste, VI, 1898, p. 115; Hazen, Bull. Torrey Bot. Club, XLIX, 1922, p. 123 et seq.

reprod. by div. of protoplast during rest; sex. reprod. almost isogamous, gametes with a thin membrane which is cast off during fusion; zygosp. unknown.

The only record for this country is *L. pentagonia* Hazen (10–13 l.: 9–10 br.) (fig. 6, A–C) from Ham Common, Surrey; its cells appear pentagonal in side-view, but end-views show 5–8 protuberances, not all on the same level. Species of this genus are likely to be overlooked owing to their small dimensions.

Brachiomonas Bohlin, 1897[1]. Unicellular; cells with a thin wall provided with one posterior and usually several anterior

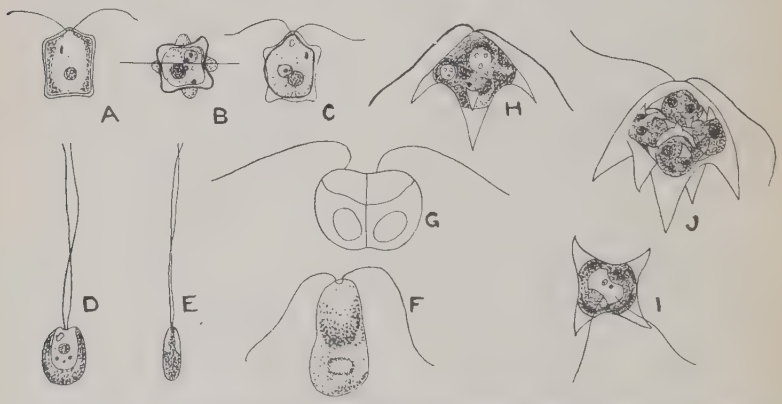

Fig. 6. A–C, *Lobomonas pentagonia* Hazen (after Hazen, ×830): A and C, front-views; B, anterior view. D, E, *Scourfieldia complanata* G. S. West (after West, ×1400), from Leyton Flats, Essex; D, front; E, side-view. F, G, *Dunaliella salina* (Dunal) Teodoresco (after Teodoresco, × 720); G, a stage in division. H–J, *Brachiomonas submarina* Bohlin (after West, ×720), from Sheerness; H, front-view (cilia shown too thick); I, anterior view; J, formation of autospores.

backwardly directed hollow horns into which the chloropl. may or may not extend. Chloropl. parietal, not always well defined; pyren. often anterior and lateral, on the side next the stigma. Contr. vacs. absent. Asex. reprod. during movement, with formation of four or eight individuals which acquire their distinctive form before liberation (autospores). Gametes often slightly anisogamous, naked, smaller and commonly simpler in form than the vegetative cells. Zygosp. spherical, smooth.

Two Brit. sp. are recorded, viz. *B. submarina* Bohlin (15–24 l.: 13–25 br.) (fig. 6, H–J) and *B. simplex* Hazen (30–48 l.: 18–24 br.),

[1] Bohlin, 1897 *a*, p. 508; West, 1908, p. 281; Hazen, Bull. Torrey Bot. Club, XLIX, 1922, p. 75.

the latter differing from the former *inter alia* in the absence of the anterior horns. They seem to favour rock-pools with brackish water, although the former sp. has been recorded from freshwater habitats[1].

Scourfieldia G. S. West, 1912[2]. Unicellular: cells minute, elliptic-ovate in front-view, strongly compressed, with a thin wall and cilia about four times the length of the cell, movement in one sp. at least backwards. Chloropl. bell-shaped, without pyren. or stigma: starch apparently lacking. Reprod. unknown.

Only two sp. are known, viz. *S. complanata* G. S. West (5·2–5·7 l.: 4·4–4·6 br.) (fig. 6, D, E) with an oblong side-view, and *S. cordiformis* Takeda (4–4·5 l.: 3·5–4 br.) with an obovate side-view, the cilia of both being about 20 μ long.

Dunaliella Teodoresco, 1905[3]. Unicellular: cells ellipsoid, often with a median waist, naked and subject to slight changes of shape. Chloropl. typical: haematochrome often present: no contr. vacs.: stigma present or absent. Asex. reprod. by longit. div. during movement, each new individual forming one cilium afresh. Gametes isogamous: zygosp. thin-walled, producing four individuals on germination.

D. salina (Dunal) Teodoresco (=*Haematococcus salinus* Dunal. *Chlamydomonas Dunalii* Cohn: 18–23 l.; 8·5–12 br.) (fig. 6, F, G) has been recorded from brackish pools in Cornwall (West, 1915, p. 73).

Polytoma Ehrenberg, 1831[4]. Unicellular: cells ovoid, with a thin wall devoid of a beak. Chloropl. absent, but starch-grains often abundant: stigma and contr. vacs. present. Asex. reprod. by div. during movement. Gametes almost isogamous: zygosp. round, smooth.

P. uvella Ehrenb. (=*Chlamydomonas hyalina* Cohn; 10–20 l., 6–12 br.) (fig. 4, F) is probably widely distributed in waters harbouring much decaying organic matter, but has so far rarely been recorded in this country (cf. Grove, 1920, p. 23).

Gonium Müller, 1773[5] (incl. *Tetragonium* W. & G. S. West, 1896). Coenobium a flat plate of 4 or 16 ovoid or slightly polygonal cells separated by triangular inter-spaces and connected by protoplasmic processes at the points of contact (always?).

[1] Neilson-Jones, Proc. Linn. Soc., 1922, p. 57; Tozer, Journ. Roy. Microscop. Soc., 1908, p. 551.

[2] West, 1912, p. 326; Takeda, Ann. of Bot. xxx, 1916, p. 157.

[3] Teodoresco, Beih. Bot. Centralbl. xviii, 1905, p. 215, and Rev. gen. de Bot. xviii, 1906, p. 353; Hamburger, Archiv f. Protistenk. vi, 1905, p. 111.

[4] cf. Dangeard, Ann. sci. nat., 7 sér. vii, 1888, p. 112; Dangeard, Le Botaniste, viii, 1901, p. 5; Entz, Archiv f. Protistenk. xxxviii, 1918, p. 324.

[5] cf. Warming, Bot. Tidsskr. ix, 1876, p. 69; Migula, Bot. Centralbl. xliv, 1890, p. 72; Harper, Trans. Amer. Micr. Soc. xxxi, 1912, p. 65.

sometimes with a common mucilage-investment; cilia all directed to one side. Chloropl. typical; contr. vacs. and stigma present. Asex. reprod. by formation of daughter-coenobia within each cell of parent, rarely by zoosp. (four per cell), or by dissociation of coenobium. Gametes isogamous, 16 per cell; zygosp. with a smooth or rough membrane, producing four zoosp. on germination.

G. pectorale Müll., which has a square coenobium with truncated corners, composed of 16 cells (4 central, 12 peripheral; 7–11 br.)

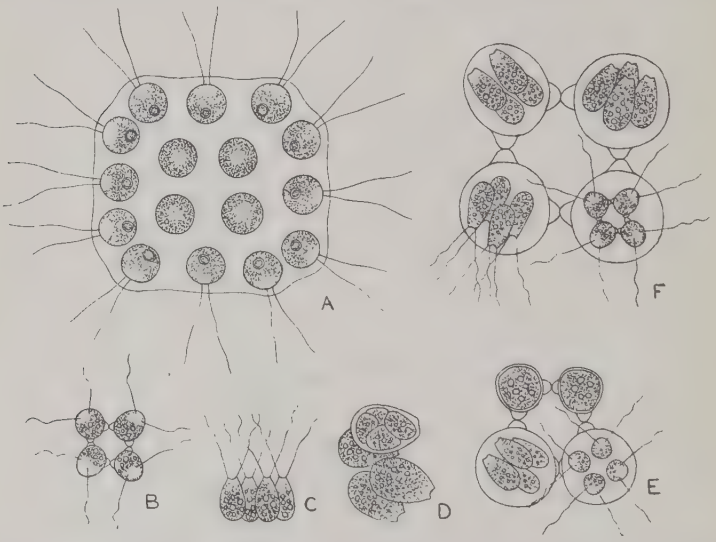

Fig. 7. A, *Gonium pectorale* Müll., from Cambridge. B–F, *G. sociale* (Duj.) Warming, from Esher Common, Surrey. E and F show the formation of new coenobia (×475).

(fig. 7, A), is frequent in stagnant ditches and ponds. *G. sociale* (Duj.) Warming (*G. lacustre* West, *Tetragonium lacustre* W. & G. S. West[1]) (fig. 7, B–F) has 4-celled coenobia, the ovoid cells of which are 11·5–19 l. and 7·5–15·5 br. The anterior end of each cell is somewhat protracted and the cilia are only vibratile towards their extremities (always?), the movements being correspondingly sluggish. This sp. is much rarer than *G. pectorale* and prefers the open waters of large ponds and lakes.

Pandorina Bory, 1824[2]. Coenobia spherical or subspherical, usually of 16 (rarely 8 or 32) closely packed pyriform cells, whose

[1] West and West, 1896, p. 160.

[2] Pringsheim, Monatsber. d. K. Akad. d. Wiss., Berlin, 1869, p. 724; Dangeard, Le Botaniste, VII, 1900, p. 192.

broader end faces outwards and which reach almost to the centre, the whole surrounded by a mucous investment; cells often angular as the result of mutual pressure, typically Chlamydomonad in structure, each with two widely divergent cilia, cells at the anterior pole with larger eye-spots. Asex. reprod. by formation of daughter-coenobia within each cell of parent, prior to which the cells of the latter round off and separate somewhat; also, but rarely, by liberation of single swarmers. Gametes formed by div. of protoplasts into 16 or 32 parts, often aniso-

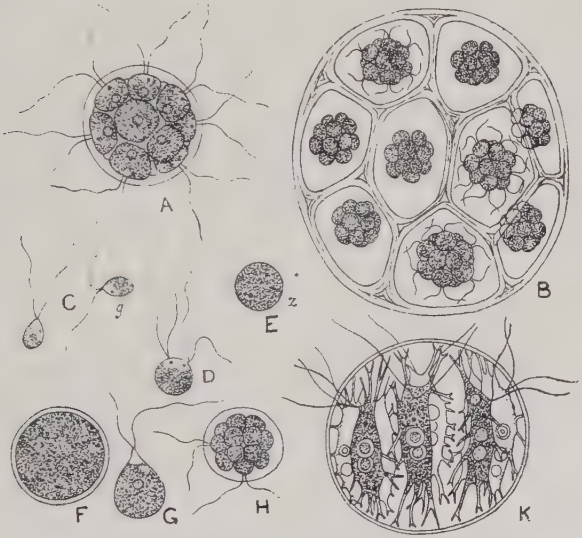

Fig. 8. A–H, *Pandorina morum* (Müll.) Bory; A, adult coenobium; B, group of daughter-coenobia within the swollen investment of the parent; from near Bradford, W. Yorks (×475). C–H, formation of zygospore (z) and its development (after Pringsheim). K, *Stephanosphaera pluvialis* Cohn (after Hieronymus, ×320). g, gamete.

gamous; zygosp. smooth, giving rise on germination to a new coenobium.

P. morum (Müll.) Bory is abundant in ponds and ditches all over the country (cells 8–15 br. and coenobia 20–42 in diameter) (fig. 8, A–H).

Eudorina Ehrenberg, 1832[1]. Coenobium globose or ellipsoid, of usually 32 cells (4 anterior, 4 posterior, and three intervening series of 8), loosely arranged in the periphery of a mucous

[1] Goebel, Grundz. d. Syst. u. spec. Pflanzenmorph., Leipzig, 1882, p. 41; Conrad, Rec. Inst. Bot. Bruxelles, IX, 1913, p. 321.

investment and connected by delicate protopl. strands only to be seen after staining (Conrad); cells globose with the usual Chlamydomonad structure, but often with several pyrenoids, and showing a progressive decrease in size of eye-spots from front to back. Asex. formation of daughter-coenobia as in *Pandorina* from all the cells of the parent. Sex. reprod. oogamous, coenobia usually dioecious; the slightly enlarged cells of the female coenobia form the ova, each cell of the male produces a flat plate (fig. 9, E) of 64 fusiform or pear-shaped spermatozoids; oosp. smooth, producing a new coenobium on germination.

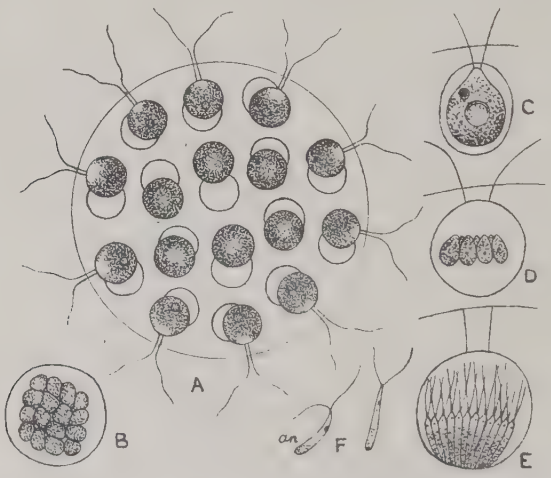

Fig. 9. *Eudorina elegans* Ehrenb. A, adult coenobium (×475); B, young coenobium formed by division of protoplast of parent-cell (×730), from Frizinghall, W. Yorks. C–E, development of spermatozoid-clusters; F, spermatozoids (after Goebel).

E. elegans Ehrenb. is widely distributed in ponds, ditches, and lakes, being fairly general in the plankton, especially in autumn: cells 10–25 br. and coenobia 40–150 in diameter (fig. 9). It appears that there are two forms of this sp., the one with globose, the other with ellipsoid or even ovate-ellipsoid coenobia; the latter also differ from the former in the presence of several mucous mammillate projections at the posterior pole. In this country the globose form is that generally found.

G. S. West (1904, p. 194) at one time regarded Lemmermann's genus *Eudorinella*[1] as synonymous with *Eudorina*, but subsequently (1916 *a*, p. 182) followed Wille (1909, p. 20) in referring it to Schewiakoff's *Stephanoon*. Here the cells are arranged in two planes within

[1] Lemmermann, Ber. Deutsch. Bot. Ges. XVIII, 1900, p. 307; Fritsch, 1918, p. 492.

a spherical or ellipsoidal mucilage-envelope. The genus is at present not recorded for this country.

Pleodorina Shaw, 1894[1]. Coenobium spherical or ellipsoidal, of 32, 64, or 128 ovoid or spherical cells, arranged at a slight distance from one another in the periphery of a mucous investment; mature coenobium differentiated into smaller vegetative

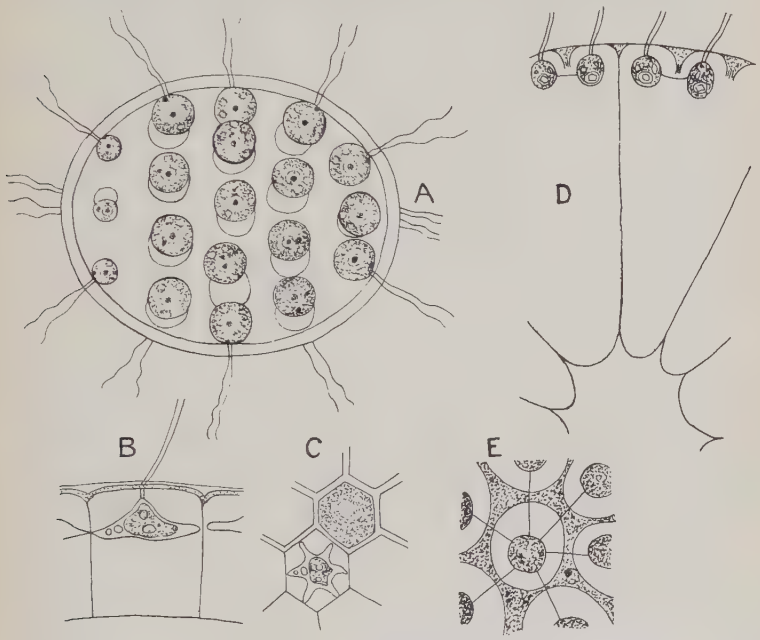

Fig. 10. A, *Pleodorina illinoiensis* Kofoid (after Kofoid, ×300). B–C, *Volvox globator* Ehbg., small parts of coenobia, diagrammatic (after Meyer); B, in section; C, in surface view. D–E, *V. aureus* Ehbg., portions of coenobium, diagrammatic (after Meyer); D, section; E, surface view (firm membranes and protoplasts dotted).

and larger reprod. cells (gonidia). Chloropl. typical, with a single pyren.; eye-spots as in *Eudorina*. Asex. formation of daughter-coenobia usually restricted to the gonidia. Sex reprod. as in *Eudorina*, but spermatozoid-plates sometimes comprising 128 cells.

There are two sp.: *P. illinoiensis* Kofoid with usually 32-celled coenobia (max. dimens. 200 × 175), the cells grouped as in *Eudorina*,

[1] cf. Shaw, Bot. Gaz. XIX, 1894, p. 279; Kofoid, Ann. and Mag. Nat. Hist., ser. 7, VI, 1900, p. 139; Merton, Zeitschr. f. wiss. Zool. XC, 1908, p. 445; Chatton, Bull. scient. France et Belgique, XLIV, 1910, p. 309; Grove, New Phyt. XIV, 1915, p. 169.

4 vegetative and 28 gonidial (fig. 10, A); and *P. californica* Shaw with 64 or 128 cells in the coenobium (diam. 175–300), from one-half to two-thirds of them becoming gonidial. Both have been found in the Brit. Isles. Messrs. West have referred to the latter sp. specimens from Loch Fadaghoda, Lewis, in which the coenobia comprised only 32 cells, about half of them being vegetative (West and West, 1905, p. 506). Various writers have suggested that *Pleodorina* is merely a form of *Eudorina elegans* (Chodat, 1902, p. 152; West and West, 1906, p. 105), but the common strains of the latter certainly never show the sharp differentiation between vegetative and reprod. cells which is characteristic of *Pleodorina* (cf. also Grove, loc. cit. p. 181; Smith, 1920, p. 97)[1].

Sub-family 2. Carterieae

Individuals quadriciliate.

Carteria Diesing, 1868[2] (*Pithiscus* Dangeard, 1888; *Corbicra* Dangeard, 1888). Unicellular; cells spherical, ellipsoid, or cordiform, differing from those of *Chlamydomonas* solely in the possession of four instead of two cilia.

There are five Brit. sp. of this genus which is considerably rarer than *Chlamydomonas*. *C. multifilis* (Fresen.) Dill, with rounded cells (10–16 br.) and cilia inserted in pairs, is fairly abundant in small pools, more particularly those of rain-water (fig. 5, A–G). Other forms sometimes encountered are: *C. obtusa* Dill with cylindrical-elliptical cells and the pyrenoid situated *in front* of the nucleus, and *C. cordiformis* (Cart.) Bütschli with heart-shaped cells (9–16 br.: 12–20 l.).

The interesting colonial genus *Spondylomorum*[3], with 16 obovate cells disposed in four alternating tiers of four, has not yet been found in this country. Jacobsen (loc. cit.) has recorded it in Dutch soils.

Family 3. SPHAERELLACEAE

The motile forms of this family are in all cases biciliate. The cell-wall (except *Chlorogonium*) is usually thick and differentiated into a superficial firmer layer and an extensive gelatinous zone, generally traversed by strands from the central protoplast. The chloroplast occupies a great part of the periphery of the latter and is often not well defined; there are several scattered pyrenoids and usually more than two contractile vacuoles which are

[1] With regard to Shaw's genera *Copelandosphaera* and *Merrillosphaera*, see under *Volvox*.

[2] cf. Goroschankin, loc. cit.; Dill, loc. cit.; Wille, 1903, p. 89; West, 1915, p. 73; Takeda, Ann. of Bot. xxx, 1916, p. 369.

[3] Ehrenberg, Monatsber. Berlin Akad., 1848, p. 236.

dispersed through the protoplasm. The reproductive processes are very similar to those of Chlamydomonadaceae.

Sphaerella Sommerfeldt, 1824[1] (*Haematococcus* Agardh, 1828; *Chlamydococcus* A. Braun, 1849). Unicellular; cells ovoid, sometimes with a beak between the two cilia. Chloropl. peripheral, more or less reticulate, with 2–8 scattered pyrens.; numerous contr. vacs. in the periphery of the protoplast; single eye-spot; bright red haematochrome often abundant, both in motile and resting stages. Asex. reprod. during movement. Sex. reprod. isogamous, as many as 100 gametes being formed from one individual. Spherical resting cells (cysts), with a thick cellulose wall and deep red contents, are readily formed from the motile individuals by contraction and rounding off of the protoplast at one or other end of the cell. *Palmella*-stages known.

S. lacustris (Girod.) Wittr. (*Chlamydococcus pluvialis* (Flot.) A. Br.: *Haematococcus pluvialis* Flotow) (fig. 11) is abundant all over the country in ditches, rain-pools, and bog-pools; its cells (8–30 br.) are often brick-red in colour and very readily form cysts, and "red rain" is sometimes due to this Alga. No gametes have been observed in this sp. It is the only one recorded for the British Isles, but a form resembling *S. droebakensis* (Wollenweber) has been observed in material from Wales.

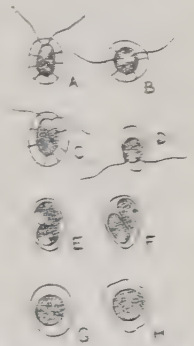

Fig. 11. A–H. *Sphaerella lacustris* (Girod.) Wittr., from Bradford, W. Yorks (×475).

Chlorogonium Ehrenberg, 1830[2] (*Cercidium* Dangeard, 1888). Unicellular; cells fusiform, three or more times longer than the diameter, with a thin closely adhering wall. Chloropl. more or less plate-shaped and unilateral, often ill-defined, spongy, with 4–many pyrens.; several (12–16) contr. vacs. scattered through the protoplast. Asex. reprod. by two successive transv. divs. during movement, the products later lying parallel to one another. Gametes (16–32 per cell) often anisogamous; zygosp. spherical, smooth, with reddish-brown contents.

[1] cf. Hazen, Mem. Torrey Bot. Club, VI, 1899, p. 211; Schmidle, Ber. Deutsch. Bot. Ges. XXI, 1903, p. 346; Peebles, Centralbl. f. Bakt. XXIV, 1909, p. 511; Wollenweber, Ber. Deutsch. Bot. Ges., Festschr. XXVI, [illegible] p. 238; Mevius, ibid. XLI, 1923, p. 237. With regard to Wille's views on the nomenclature of this genus, see Wille, 1903, p. 94.

[2] cf. Dangeard, Le Botaniste, VI, 1898, p. 79; Bohlin, 1897, p. 511; Schmidle, loc. cit. p. 348.

C. euchlorum Ehrenb. (8–12 br.; up to 50 l.) (fig. 4, G–H) is rather scarce, being found in stagnant waters; Jacobsen (loc. cit.) has found it in cultures of certain types of soil. Its systematic position is doubtful. Schmidle has drawn attention to the approximation between certain sp. of *Chlorogonium* and *Chlamydomonas*[1].

Stephanosphaera Cohn, 1852[2]. Coenobium usually of eight cells, arranged in an equatorial zone within a tough, spherical or ellipsoidal investment; cells elongated with several green or colourless protopl. processes, mainly at either end, the cilia penetrating the investment near the equatorial plane. Chloropl. like that of *Sphaerella*, with one anterior and one posterior pyren.; contr. vacs. numerous. Asex. reprod. by formation of a new coenobium within each cell of the parent, the cells rounding off prior to division. Gametes (8, 16, or 32 per cell) fusiform and isogamous; zygosp. spherical, yellowish-brown, giving rise to 2–8 zoosp. on germination.

S. pluvialis Cohn (cells 6–12 and coenobia 26–60 br.) (fig. 8, K) is rare, but has been recorded both in England and Ireland, being usually found in the rain-water which collects in the hollows of rocks. Young coenobia are occasionally observed containing only one or two cells.

Volvox (Linnaeus, 1758) Ehrenberg, 1830[3]. Coenobium a hollow sphere or ellipsoid, of usually very numerous (up to 25,000) cells forming a peripheral layer within the mucous investment; cells with globose, ovoid, or stellate protoplasts, often connected by protoplasmic strands which may be slender or stout; cell-walls thick and gelatinous, with firmer middle lamellae. Chloropl. probably much like that of *Sphaerella*, with one or more pyrens.; 2–6 often scattered contr. vacs.; eye-spots as in *Eudorina*. Asex. reprod. by formation of new coenobia within special gonidia (up to 25 in number) situated in the posterior part of the parent-coenobium and distinguishable at an earlier or later stage by their considerable size; the young embryos[4] are liberated into the hollow interior of the parent and

[1] cf. also Wille, 1909, p. 18, who regards *Chlorogonium* as a subgenus of *Chlamydomonas*.

[2] cf. Cohn and Wichura, Nov. Act. Leop.-Carol. xxvi, 1857, Nachtrag: Hieronymus, Cohn's Beitr. iv, 1884, p. 51.

[3] Klein, Jahrb. Wiss. Bot. xx, 1889, p. 133, and Ber. Deutsch. Bot. Ges. vii, 1889, p. 42; Overton, Bot. Centralbl. xxxix, 1889, p. 65; Meyer, ibid. lxiii, 1895, p. 225, and Bot. Zeit. liv, 1896, p. 187; Janet, Le *Volvox*, Limoges, 1912; Crow, New Phyt. xvii, 1918, p. 151; Harper, Mem. Brooklyn Bot. Gard. i, 1918, p. 154.

[4] According to Kuschakewitsch (Bull. Acad. Sc. d. l'Oukraine, i, 1922, p. 31; cf. Zeitschr. f. Bot. xv, 1923, p. 584) the young coenobia shortly before forming cilia undergo a complete invagination whereby the inner surface comes to lie outwards and the normal polarity of the cell is established.

may attain a considerable size before they are set free by the death of the latter. Sex. reprod. oogamous, coenobia monoecious or dioecious, the same individuals with or without gonidia; spermatozoids fusiform, biciliate, with pale green or yellowish chloropl. (fig. 12. C), formed in plates or spherical masses by div. of the contents of special enlarged cells; ova few, rounded, appearing as much enlarged cells, often with a neck-like protrusion; oosp. spherical, with smooth, or substellate membrane and brownish-red contents, germination direct.

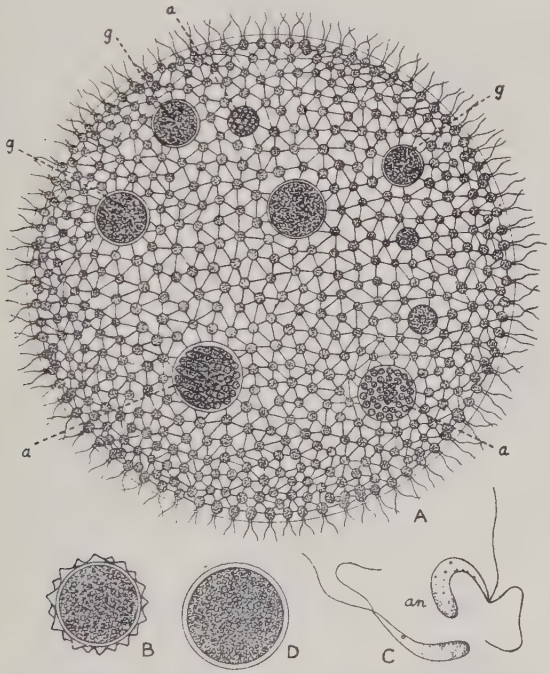

Fig. 12. A, C, and D, *Volvox aureus* Ehrenb. A, monoecious sexual colony (×210), from Rawcliffe Common, W. Yorks; D, ripe oospore (×475); C, two spermatozoids (after Klein). B, ripe oospore of *V. globator* (L.) Ehrenb., from Preston, Lancashire (×475). *a*, antheridia; *an*, spermatozoid; *g*, ovum.

Shaw[1] has undertaken a comprehensive investigation of the various sp. of *Volvox* and advocates the establishment of a number of genera, as follows:

(*a*) Without intercellular protoplasmic strands.

1. *Copelandosphaera*, in which the gonidia are not differentiated in

[1] Philippine Journ. Sci. xv, 1919, p. 493; xx, 1922, p. 477; xxi, 1922, pp. 87 and 207; xxii, 1923, p. 185.

the young embryos and attain some size before segmentation sets in; monoecious.

2. *Merrillosphaera*, in which the gonidia are differentiated in the young embryos, are arranged in pairs or fours, and at an early stage sink from their positions in the somatic layer, so as to lie within the embryo coenobium; dioecious.

(*b*) With intercellular protoplasmic strands.

1. *Janetosphaera* with round protoplasts, cells without distinct internal walls; usually dioecious (fig. 10, D).

2. *Volvox* with stellate protoplasts, cells with distinct internal walls; monoecious (fig. 10, B).

The suggestion is that *Copelandosphaera* and *Merrillosphaera* belong to the Chlamydomonadaceae and the other two genera to the Sphaerellaceae, but unfortunately the details of cell-structure are imperfectly known in the case of the former. While it is not improbable that the *Volvox*-type of coenobium may have originated separately in the two lines, the resemblances being due to homoplasy, the evidence does not at the present time appear sufficient to warrant the generic splitting proposed by Shaw.

Three sp. of *Volvox* have been recorded in the Brit. Isles. *V. aureus* Ehrenb. (*Janetosphaera aurea* Shaw) and *V. globator* Ehrenb. are common in deeper ponds and ditches of the low-lying areas, being often associated with *Lemna* and preferring ponds which receive a plentiful supply of rain-water. In *V. aureus* (fig. 10, D, E; fig. 12, A, C, D) the adult coenobia are 200–500 μ in diameter, the protoplasts are rounded and connected by extremely delicate processes, and the walls of the oosp. are smooth. *V. globator* is usually larger (680–800 μ in diam.), the protoplasts are stellate with thick processes, and the ripe oosp. are substellate (fig. 12, B; fig. 10, B, C). *V. mononae* G. M. Smith[1], in which cytoplasmic processes are lacking, is known from the plankton of the Lake District[2].

The Rotifer *Notommata parasitica* sometimes occurs as a parasite within the hollow coenobia of *Volvox*, swimming about within the central cavity and feeding on the green cells either of the adult or of the daughter-coenobia.

Family 4. PHACOTACEAE

The outstanding characteristic of this family of biciliate unicellular organisms is the presence of a specialised envelope, which is thick and sometimes composed of two valves; in most cases it is separated from the contained protoplast by a space, but whether there is a distinct cell-wall apart from the envelope is mostly uncertain. Where the cell-structure is known, it is of

[1] G. M. Smith, 1920, p. 99, Pl. XVIII, fig. 1; the chloropl. is described as bell-shaped with a single pyrenoid, which would certainly relate this form to the Chlamydomonadaceae.

[2] Pearsall, Journ. Linn. Soc., Bot. xlvii, 1925, p. 72.

the Chlamydomonad type, although often with several pyrenoids. Asexual reproduction is effected by successive division of the protoplast, the daughter-individuals before liberation acquiring the characteristics of the parent. Sexual reproduction is only certainly established in one genus.

Phacotus Perty, 1852[1]. Cells considerably flattened, so that they appear circular or oval in front- and biconvex in side-view; envelope thick, dark-coloured, calcified, rough, composed of two valves with somewhat thickened rims fitted together like two watch-glasses; protoplast ovoid, usually separated from envelope except at front end by a considerable space (occupied by mucilage?); cilia emerge through fine canals in the thickened rim of the envelope. Asex. reprod. by div. of protoplast into 2–8 parts within a mass of mucilage separating the valves of the parent (fig. 13, A); each daughter-individual acquires the bivalved envelope prior to liberation.

P. lenticularis (Ehrenb.) Stein (*Cryptoglena lenticularis* Carter; 13–17 l.) (fig. 13, A–C) is not uncommon in stagnant water. It is not clear from the available data whether there is a cell-wall distinct from the envelope. The sexual reproduction described by Carter[2] is probably a misinterpretation.

Pteromonas Seligo, 1886[3]. Cells of varied shape, strongly compressed, with a bivalved silicified (always?) envelope which is broadly winged in the plane of junction of the two valves (fig. 13, D, F) whose joined rims form a straight or slightly curved suture; protoplast spherical or ovoid, at most points in close contact with the envelope; chloropl. cup-shaped, with 1–6 pyrens. Asex. reprod. much as in *Phacotus*, with production of 2–4 new individuals. Gametes isogamous; zygosp. spherical, brown.

Five sp. of this genus are now known to occur in ponds and lakes in the Brit. Isles, but they are decidedly rare. The most frequent is *P. angulosa* (Carter) Dang. (*Cryptoglena angulosa* Carter; 15–17 l.: 15·5–17 br.) (fig. 13, D, E) with a rounded wing and a protoplast which in side-view is seen to be deeply hollowed out at four points. In *P. Chodati* Lemm. (*P. angulosa* Chod.) the wing is hexagonal (19 l.: 21 br.) and the envelope in side-view shows two large papillae on either side.

[1] Dangeard, Le Botaniste, I. 1889, p. 144 and VI, 1898, p. 118.

[2] Ann. and Mag. Nat. Hist. 3 sér. II, 1858, p. 249.

[3] Seligo, Cohn's Beitr. IV, 1886, p. 170; Golenkin, Bull. soc. imp. nat. Moscou, V, 1891, p. 417; Lemmermann, Ber. Deutsch. Bot. Ges. XVIII, 1900, p. 92; West, 1912, p. 330; West, 1916, p. 7.

Coccomonas Stein, 1878[1]. Cells with a hard, brittle, ovoid or 4-angled envelope of some thickness, provided with a single circular aperture through which the two cilia emerge; protoplast ovoid, with a distinct cell-wall, separated except at the front end by a considerable space from the envelope. Reprod. by div. of the protoplast into four parts which are liberated by irregular splitting of the envelope into two pieces.

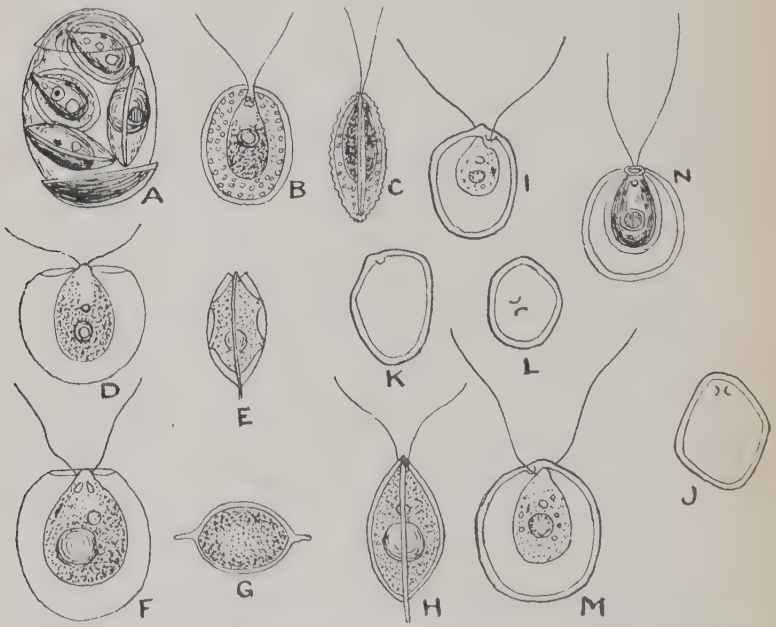

Fig. 13. A–C, *Phacotus lenticularis* Stein: A, dividing individual (after Stein, ×650); B, front-, and C, side-views (after G. S. West, ×800). D–E, *Pteromonas angulosa* (Carter) Dang.; D, front-, and E, side-views (after G. S. West, ×1000). F–H, *P. Takedana* G. S. West; F, front-, G, end-, and H, side-views (after G. S. West, ×1000). I–M, *Dysmorphococcus variabilis* Takeda, from Richmond Park, Surrey (after Takeda, ×1000); in J–L, only the empty shell is shown; J, front-, K, side-, and L, anterior-views. N, *Coccomonas orbicularis* Stein (after Stein, ×650).

C. orbicularis Stein (fig. 13, N), the only Brit. sp., has been found in artificial waters in Kew Gardens (Fritsch, 1906, p. 202). It is likely however to have a wider distribution.

Dysmorphococcus Takeda, 1916[2]. Cells with a hard, brittle, brown-coloured envelope which is more or less spherical or

[1] Stein, Organ. d. Infusionsthier. III, 1878, p. 54.
[2] Takeda, Ann. of Bot. XXX, 1916, p. 151.

broadly ovoid, but very irregular and variable in shape and easily cracking into irregular pieces: at the front end are two minute apertures through which the cilia emerge, the two apertures usually not both in the plane of the front-view; protoplast naked, pear-shaped, and separated by a wide space from the envelope. Reprod. unknown[1].

D. variabilis Takeda (fig. 13, I–M), the only sp., was found in a stagnant pool in Richmond Park, Surrey. It is a small form (envelope 14–19 l. and 13–17 br.) which might easily be confused with *Trachelomonas volvocina*. It is obviously closely related to *Coccomonas*.

Series II. CHLORODENDRALES

Family CHLORODENDRACEAE

This family includes a variety of dendroid colonial forms (cf. p. 66) which are all probably closely related to the Chlamydomonadaceae. They differ among one another in the manner of formation of the colony, in the details of cell-structure (probably always a single chloroplast), and in the characteristics of the swarmers which often play a prominent part in the life-history. Sexual reproduction has not been observed. The only genus

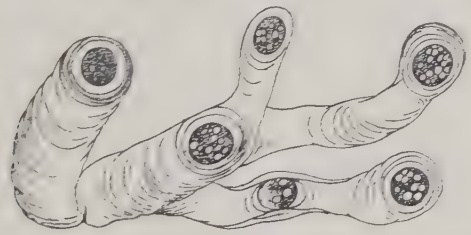

Fig. 14. ***Hormotila mucigena*** **Borzi, from Boston Spa, W. Yorks (×520).**

known in Britain is *Hormotila*, which should perhaps be placed in a separate family.

Hormotila Borzi, 1883[2]. Cells spherical, ovoid, or ellipsoid, rarely oblong, placed at irregular intervals in branched, firm, often concentrically lamellose mucilage-cylinders, which are formed between the daughter-cells after div.; the latter takes place at first in three, then in two, and finally only in one direction. Chloropl. single (?), frequently very granulose, and devoid

[1] *Isococcus* Fritsch (1914, p. 341) is a species of *Chlamydomonas* (cf. Fritsch and Takeda, Ann. of Bot. xxx, 1916, p. 373).

[2] Borzi, Studi algologici, I, 1883, p. 99.

of a pyren. (?)[1]. Reprod. by enlargement of the cells and subdivision of the contents to form 8–64 minute biciliate zoosp.

G. S. West has recorded *H. mucigena* Borzi (fig. 14) from Boston Spa, W. Yorks, where it formed an expanded dull green stratum on damp calcareous rocks; br. of veget. cells 4–12, of zoosporangia up to 30; zoosp. 1–2·5 br. and 3–5 l. M'Keever found it in a damp hothouse, Leith, Scotland. The published accounts of the cell-structure are not in agreement. Chodat (1902, p. 285) has described "*Hormotila*-stages" of a sp. of *Pleurococcus*, but these have not been confirmed.

Series III. TETRASPORALES

Family 1. PALMELLACEAE

In the members of this family the ordinary vegetative cells are embedded, often in large numbers, within a structureless or stratified mass of mucilage, which is of indefinite extent except in a few genera. The chloroplast is in many cases of the Chlamydomonad type, but a pyrenoid is wanting in some genera. The wall of the individual cell is thin and firm. Motile biciliate reproductive cells, which are mostly asexual, have been observed in some cases. The family is almost certainly not natural.

Palmella Lyngbye, 1819; emend. Chodat, 1902[2]. Cells spherical, surrounded by mucous coats which fuse to form an indefinite mucilaginous mass, often of macroscopic dimensions; div. in three directions. Chloropl. bell-shaped, sometimes reddish, with a pyren. Asex. reprod. by macrozoosp. formed singly and by microzoosp. formed 4–16 in a cell. Gametes isogamous. Akinetes with a thick granulated membrane also known.

One of the few true sp. of this genus is *P. miniata* Leibl. which occurs as a mucous expansion of a brick-red colour on damp ground, wet rocks, etc.; cells 3–5 br. (fig. 2, E). *P. mucosa* Kütz. (cells 6–14 br.) and *P. hyalina* Bréb. (cells 1 μ and less in diam.) are aquatic sp., the former olive-green, the latter green in colour; the former was regarded by Chodat (1902, p. 110) and G. S. West (1904, p. 240) as a possible stage of *Tetraspora*. Many of the "species" certainly belong to the life-cycle of other Algae.

Palmodictyon Kützing, 1845[3] (incl. *Palmodactylon* Naegeli, 1849). Differs from *Palmella* mainly in the definite form of the

[1] West, 1904, p. 205 describes the chloroplast as above; Wille, 1897, p. 50, speaks of several chloroplasts without pyrenoids; Lemmermann, 1915, p. 27 writes "Chromatophoren zahlreich (?), wandständig. Pyrenoid vorhanden."

[2] Chodat, 1902, p. 110.

[3] Naegeli, 1849, p. 69; Salisbury, Trans. Herts Nat. Hist. Soc. xv, 1914, p. 125.

envelope which appears as a branched mucilage-cylinder, in some sp. structureless, in others showing a slight concentric stratification around the individual cells. Chloropl. single[1], parietal, spherical or irregularly lobed, with or without a pyren. Reprod. imperfectly known, by biciliate zoosp. and akinetes with brown walls.

The differences between *Palmodictyon* and *Palmodactylon* do not appear sufficient to warrant generic separation (cf. also Lemmermann, 1915, p. 35).

The three Brit. sp. are relatively rare forms, usually found in

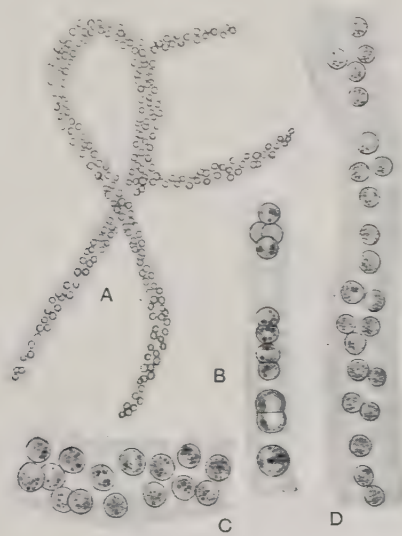

Fig. 15. *Palmodictyon varium* (Naeg.) Lemm., A–C, from Esher Common, Surrey; D, from Strensall Common, N. Yorks. A × 100; B–D × 450.

stagnant pools. *P. varium* (Naeg.) Lemm. (*Palmodactylon varium* Naeg.; *P. subramosum* Naeg.) (fig. 15) is the commonest, occurring in peaty ditches and in bog-pools; here the mucilage is structureless and the branches of the cylindrical investment (diam. 11·5–33; cells 6·5–9·5 br.) do not anastomose. In *P. viride* Kütz. this is a marked feature and the mucilage-envelope, which sooner or later assumes a reddish-brown colour, often shows some stratification around the cells (5·5–9 br.; diam. envelope, 28–52); the only method of reproduction known in this sp. is by akinetes which on germination form a new colony.

[1] cf. however Lemmermann, 1915, p. 35, who gives: "Mehrere scheibenförmige, gebogene Chlorophoren."

Sphaerocystis Chodat, 1897[1]. Cells globose, sparsely aggregated (1–2–8–16, up to several hundreds) within the periphery of a free-floating globular mass of very transparent mucilage, sometimes showing faint lamellation immediately around the cells. Chloropl. bell-shaped with pyren. Multipl. of cells by div. into four, the products being grouped either in one plane or tetrahedrally. Reprod. by formation of micro-colonies from the contents of a cell (often accompanied by a partial persistence of the parent cell-membranes, as in *Schizochlamys*, p. 92), by spherical akinetes, and by biciliate macro- and micro-zoosp.; gametes unknown.

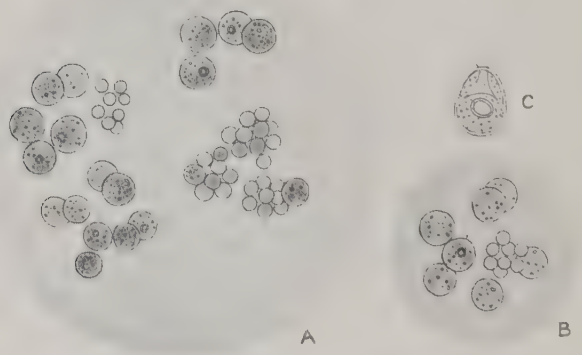

Fig. 16. *Sphaerocystis Schroeteri* Chod.: A and B, from the plankton of Loch Shin, Sutherland, × 450; C, zoospore, after Chodat (× about 700).

S. Schroeteri Chod. (*Glococcus Schroeteri* (Chod.) Lemm.) (fig. 16) is an abundant Alga, occurring in the plankton of all the larger lakes and not uncommon in smaller pieces of water; colonies 50–1200 and cells 6–10 br. It shows considerable resemblance to *Tetraspora lacustris* Lemm.[2], but at present the pseudocilia of the latter have not been demonstrated in *Sphaerocystis* and there are other differences apparent in the mode of formation of the daughter-colonies. The reference of *Sphaerocystis* to A. Braun's *Glococcus*, advocated by Wille and Lemmermann[3], cannot be regarded as sufficiently established[4].

[1] Chodat, 1897, p. 292; Chodat, 1902, p. 114.

[2] cf. Chodat, 1902, p. 115; G. S. West, Journ. Linn. Soc., Bot. xxxix, 1909, p. 75.

[3] Wille, 1903, p. 163; Lemmermann, 1915, p. 31.

[4] cf. also Chodat, Bull. Herb. Boissier, 2 sér. iv, 1904, p. 233.

Coccomyxa Schmidle, 1901[1]. Cells ellipsoid or oval, single or embedded in structureless mucilage to form microscopic or macroscopic colonies. Chloropl. a parietal plate, occupying one side of the cell with or, evidently more commonly, without a pyren.; cell-wall thin. Reprod. by div., usually in a plane oblique to the longit. axis.

The position of this genus is at present difficult to determine and some would doubtless prefer to place it among the non-zoosporic Chlorococcales (p. 96). Pascher (1915, p. 208) suggests that its sp. are not congeneric and that some may belong to Heterokontae, a view supported by the usual absence of pyrens. and the frequent yellow-green colour. In this country only the terrestrial sp., and not the planktonic ones, have so far been recorded. Three are known, viz. *C. dispar* Schmidle (cells 4–8 br., up to two and a half times as long) (fig. 17, A–C) found by the writer on damp bark or Mosses near the bases of woodland trees; *C. Solorinae* Chod. (cells 3–3·5 br.; 6–7 l.) found in cultures from cultivated soils (Bristol, 1920, p. 73); and *C. subellipsoidea* Acton (cells 4–6 br.; 6–10 l.) (fig. 17, D). Considerable doubts have been expressed whether the zoosp. recorded for the last-named sp. really belong to it (cf. Chodat, 1913, p. 224; Pascher, 1915, p. 211). Species of this genus form the algal constituent of the Lichen *Solorina* (found by the writer both in *S. crocea* and *S. saccata*: cf. also Chodat, 1913, p. 224).

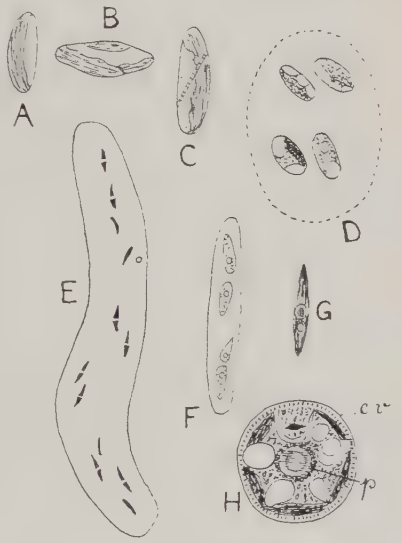

Fig. 17. A–C, *Coccomyxa dispar* Schmidle (after Schmidle); C, a dividing cell. D, *C. subellipsoidea* Acton (after G. S. West, ×750). E–G, *Elakatothrix gelatinosa* Wille (after Wille); E, young colony (×180); F, 4-celled colony (×425); G, single cell (×600). H, *Asterococcus superbus* (Cienk.) Scherffel (after Scherffel, ×580); *cv*, contractile vacuoles; *p*, pyrenoid.

The genus *Botrydina* de Brébisson, 1839, of which *B. vulgaris* Bréb. occurs among Mosses on damp ground, on the trunks of trees, etc.,

[1] Schmidle, Ber. Deutsch. Bot. Ges. XIX, 1901, p. 20; Acton, Ann. of Bot. XXIII, 1909, p. 573; Wille, Nyt Mag. f. Naturvidensk. XLVIII, 1910, p. 298; Chodat, 1913, p. 224.

has been shown by Acton[1] to be a Lichen, of which *C. subellipsoidea* Acton is the algal component in the case of the sp. just named (cf. also Pascher, 1915, p. 211).

Elakatothrix Wille, 1898[2] (*Fusola* Snow, 1903). Cells fusiform or bacilliform, arranged in rows or more irregularly within a structureless mucilage-envelope, often with a tough limiting layer. Chloropl. parietal, occupying most of the length of the cell, with a large pyren. Reprod. by transv. div. and by brown-coloured akinetes.

E. gelatinosa Wille (cells 3–4 br.; 16–25 l.) (fig. 17, E–G) is a rare plankton-Alga that has been found in some of the Brit. lakes and in a clay-pit near Durham.

Asterococcus Scherffel, 1908[3]. Cells globose or subglobose, singly, or in groups of 2–4 within very wide concentrically lamellose mucilage-envelopes. Cell-wall thin; chloropl. star-shaped with a central pyren. and numerous processes extending up to the cell-wall, where they are slightly expanded; two contr. vacs. and a lanceolate stigma present (fig. 17, H). Reprod. by div. and by biciliate zoosp. formed singly from the entire cell-contents.

A. superbus (Cienk.) Scherffel (*Pleurococcus superbus* Cienk.; *Gloeocystis infusionum* W. & G. S. West) (figs. 17, H and 18, A–E) is the only Brit. sp.; it has large cells (diam. 25–30), often filled with starch-grains, and a striking lamellated mucilage-envelope, that of a single cell often reaching 180 μ. In its possession of contr. vacs. and an eye-spot and the apparent ready assumption of a motile phase, it would seem to be not far removed from a flagellate stock. No form with a stellate chloropl. is however at present known among Chlamydomonadales.

Gloeocystis Naegeli, 1849[4]. Cells globose or ellipsoid, embedded in large numbers in an indefinite mass of mucilage formed from the membranes of successive mother-cells and generally showing marked stratification about the cells. Chloropl. parietal, bell-shaped, with one pyren. Biciliate zoosp. and akinetes recorded.

The most abundant of the two Brit. sp. is *G. gigas* (Kütz.) Lagerh. (*Gl. ampla* (Kütz.) Rabenh., *Chlorococcum gigas* Grun.), found in stagnant waters among other Algae; it has globose cells (10–17 br.) which are often grouped in tetrads (fig. 18, F–H). *G. vesiculosa* Naeg.

[1] Ann. of Bot. XXIII, 1909, p. 579.

[2] Wille, Biol. Centralbl. XVIII, 1898, p. 302; West and West, 1909, p. 291; Smith, 1920, p. 139.

[3] Scherffel, Ber. Deutsch. Bot. Ges. XXVI *a*, 1908, p. 762; Smith, Trans. Wisconsin Acad. Sci. XIX, 1918, p. 627.

[4] Naegeli, 1849, p. 65.

has smaller cells (4–12 br.) which are sometimes ellipsoid; it is found both in stagnant water and as an early coloniser on burnt heath. These commonly encountered forms are not altogether free from the suspicion

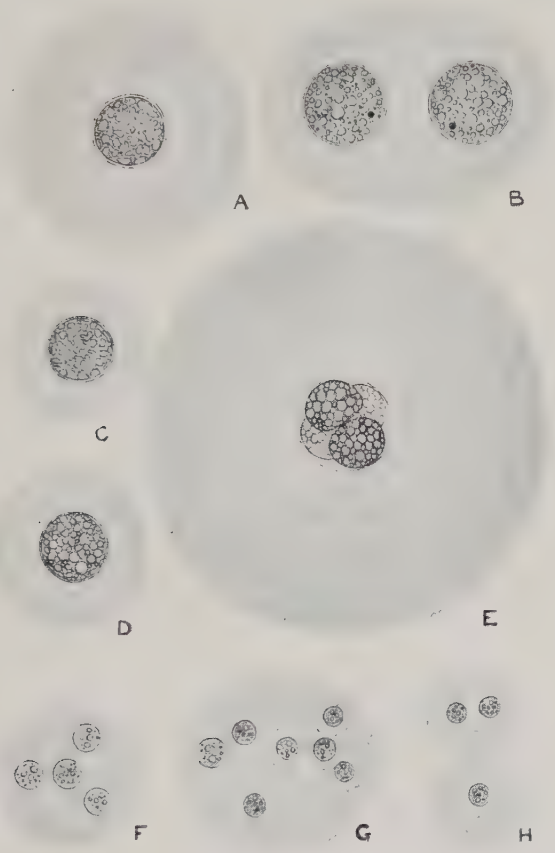

Fig. 18. A–E, *Asterococcus superbus* (Cienk.) Scherffel, from Barnes Common, Surrey. F–H, *Gloeocystis gigas* (Kütz.) Lagerh., from Wimbledon Common, Surrey. (All × 420.)

(stronger in the case of other sp. of the genus) that they belong, as *Palmella*-stages, to the life-cycles of other green Algae.

Capsulococcus Bennett, 1888[1] (with *C. crateriformis* Benn.), described from the English Lake District, is doubtful and awaits rediscovery.

[1] Bennett, Journ. Roy. Microscop. Soc., 1888, p. 3.

Dactylothece Lagerheim, 1883[1]. Closely resembling *Gloeocystis*, but with oblong-ellipsoid cells dividing only in one direction. No other method of reprod. known. Chloropl. a parietal plate occupying only about two-thirds of the cell, with or without a pyren.

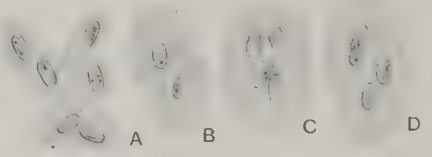

Fig. 19. *Dactylothece Braunii* Lagerh., A, from near Bradford, W. Yorks; B–D, from near Senens, Cornwall (×420).

D. Braunii Lagerh. (fig. 19) occurs in damp situations and in stagnant pools (cells 3·5 4·8 br.; 7·5 10·5 l.); the stratification of the mucilage is often obscure. Diverse opinions are held about the affinities of this Alga (cf. Pascher, 1915, p. 227; Wille, 1909, p. 71; Chodat, 1902, p. 285).

Family 2. TETRASPORACEAE

This family, which is probably more natural than the last, again comprises a number of palmelloid forms characterised by frequent grouping of the cells in fours and the possession of two or more fine protoplasmic outgrowths, the pseudocilia (cf. p. 66), arising from each cell and extending usually to the surface of the enveloping mucilage. The cells show a typical Chlamydomonad structure and their multiplication within the colonies takes place by division chiefly in two planes. The reproduction is not well known, but zoospores and isogamous gametes have been recorded in most genera.

Schizochlamys A. Braun, 1849[2]. Cells globular or slightly ellipsoid, often with a slight flattening or depression at one end, irregularly disposed within structureless mucilage; cell-wall often moderately thick, the outer portion commonly becoming ruptured (owing to mucilage-formation below it) and cast off in one or four distinct pieces which remain in the mucilage near the cells. Chloropl. with a naked pyren. (in all cases?); in one sp. two contr. vacs. near the flattened pole, but no stigma. Pseudocilia (in one sp.) of diverse length, arising in radiating

[1] Lagerheim, Öfvers. K. Sv. Vet.-Akad. Förhandl. xl, 1883, No. 2, p. 64.

[2] Kützing, Spec. Alg., p. 891; Braun, Verjüng. i. d. Natur, 1851, p. 193 (Engl. Transl. 1853, p. 181); Scherffel, Ber. Deutsch. Bot. Ges. xxvi, A, 1908, p. 783.

tufts from the flattened pole (fig. 21, D, more distinctly seen after treatment with alcohol). Reprod. by means of quadri- (rarely bi-) ciliate cylindrical or ovate zoosp., provided with an eye-spot. Gametes unknown.

There are two Brit. sp., viz.: *S. gelatinosa* A. Br. in which the membrane splits into four pieces (cells 9·5–15 br.) (figs. 20, A–B and 21, D–E), and *S. delicatula* West in which it is cast off in one piece (cells 5·8–6·7 br.) (fig. 20, C). The former occurs in very extensive gelatinous masses, often several cms. in diam., in ditches, ponds, etc., whilst the colonies of *S. delicatula* are much smaller (rarely exceeding 300 μ in diam.) and show a distinct preference for *Sphagnum*-pools; they have also been found in the plankton. *S. delicatula* requires investigation in the light of Scherffel's work on *S. gelatinosa* (loc. cit.).

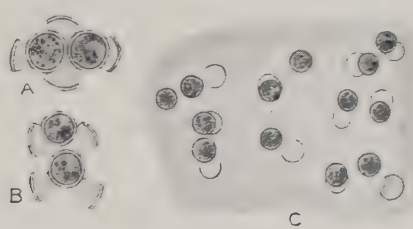

Fig. 20. A–B, *Schizochlamys gelatinosa* A. Br., from Loughrigg, Westmorland. C, *S. delicatula* West, from near Bowness, Westmorland (×450).

Tetraspora Link, 1809[1] (incl. *Stapfia* Chodat, 1897). Cells spherical, grouped irregularly or in twos and fours within the periphery of structureless mucilage to form microscopic free-floating spherical colonies or, more commonly, macroscopic, indefinitely expanded or more or less intestiniform and convoluted masses; the latter at first attached, later free-floating. Chloropl. with pyren. Pseudocilia paired, often of considerable length. Reprod. by (1) biciliate zoosp., (2) isogamous gametes forming a spherical zygosp., and (3) spherical akinetes with thick brown walls.

Of the four Brit. sp., *T. gelatinosa* (Vauch.) Desv. (incl. *T. explanata* Ag. (fig. 21, A, B)), with a vesicular gelatinous colony, later tearing open irregularly, is the commonest; cells 6–12 br. *T. lubrica* Ag., with tubular usually much lobed colonies, may be but a form of the first-named sp. (cf. West, 1904, p. 243). Both are found in stagnant waters, esp. in spring. There are two microscopic planktonic sp., viz. *T. lacustris* Lemm. (cells 7–8 br.; pseudocilia long) and *T. limnetica*

[1] Reinke, Jahrb. Wiss. Bot. XI, 1878, p. 541; West and West, 1912, p. 431; McAllister, Ann. of Bot. XXVII, 1913, p. 681.

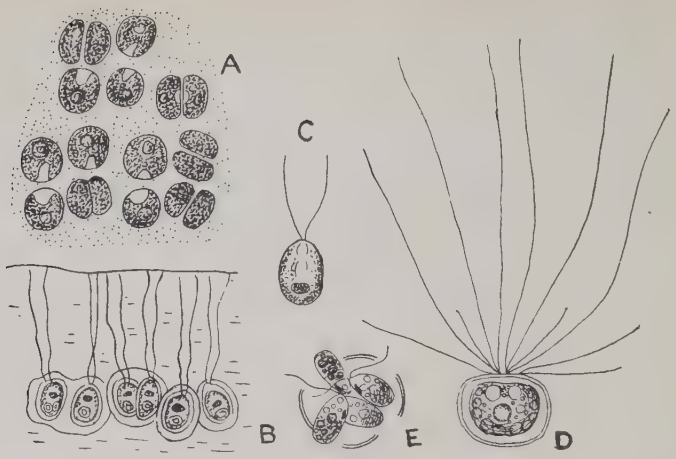

Fig. 21. A–C, *Tetraspora gelatinosa* (Vauch.) Desv.; A, small part of thallus seen from the surface (after Reinke, ×525); B, in section, showing pseudocilia (after Chodat, ×500); C, swarmer. D–E, *Schizochlamys gelatinosa* A. Br. (after Scherffel, ×560); D, single cell, the pseudocilia actually much longer; E, formation of swarmers.

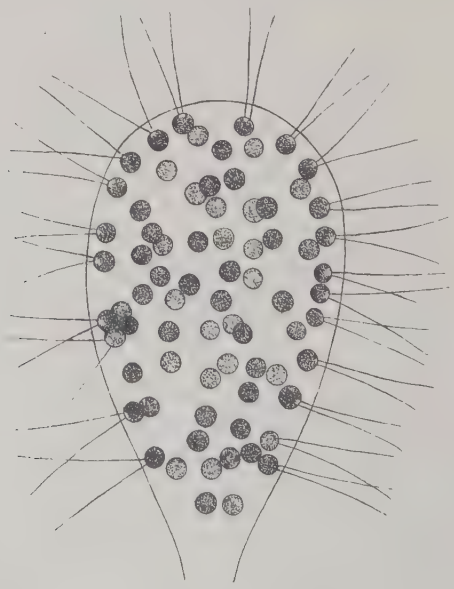

Fig. 22. *Apiocystis Brauniana* Naeg., from near Bowness, Westmorland (×400).

W. & G. S. West (cells 4 br.; pseudocilia short); the former has been suspected of being but a stage in the life-cycle of *Sphaerocystis Schroeteri* (q.v.), but the issue is undecided.

Apiocystis Naegeli, 1849[1]. Colonies small, commonly pear-shaped and epiphytic on larger Algae, the envelope usually with a well-defined firm bounding layer; cells spherical, each furnished with two pseudocilia, penetrating into the surrounding water, the projecting portions with special mucilage-envelopes of their own. Chloropl. with pyren. Reprod. by biciliate zoosp., isogamous gametes, and spherical akinetes with a thick verrucose membrane.

A. Brauniana Naeg. (colonies 12–1000 μ or upwards l.; cells 6–8 br.) (fig. 22) is not uncommon in ponds, ditches, bog-pools, etc.

GROUP 2. CHLOROCOCCALES[2]

Among the unicellular Chlamydomonadales asexual reproduction of the individual is often preceded by withdrawal of the cilia and cessation of movement. If this brief motionless phase become indefinitely prolonged at the expense of the period of free movement, in other words if the swarmer come to rest soon after its liberation and remain passive during a prolonged period of vegetative growth before renewed production of motile cells takes place, we should have realised all the essential features of a simple member of the Chlorococcales, such as *Chlorococcum* (fig. 23, C, G). Here the often spherical cells possess much the same internal structure as a *Chlamydomonas*, although lacking the special equipment (stigma, contractile vacuoles) that is ordinarily associated with the motile phase. The chloroplast is essentially the same as that of many Volvocales. It is a parietal, almost spherical structure, with an aperture at one side of the cell, a single pyrenoid being often embedded in the opposite side of the sphere. This type of cell-structure is typical of many Chlorococcales and for the sake of brevity may subsequently be referred to as "chlorococcoid." At first there is a single central nucleus, though usually as the cell enlarges both nucleus and pyrenoid multiply.

When the cells have reached a certain size successive division of the protoplast into two, four, eight, etc. parts takes place, each acquires an ovoid or oblong shape and two cilia, and then

[1] Naegeli, 1849, p. 67; Correns, Zimmermanns Beitr. z. Pflanzenzelle, Heft III, 1893, p. 241; Moore, Journ. Linn. Soc., Bot. XXV, 1890, p. 362.

[2] This corresponds to the group Protococcales of Oltmanns, Brunnthaler, etc. Since *Protococcus*, if the name be retained at all, is not a member of this group, it is deemed best to drop the old designation.

by rupture of the membrane these *naked* swarmers (zoospores) are set free (fig. 23, F); at their first liberation, as in so many of the filamentous Algae, they are often surrounded by a delicate vesicle which in a few seconds dissolves away. After a period of movement the cilia are withdrawn, the zoospore rounds off and, with the formation of a cell-membrane, a new vegetative phase is initiated. In some cases these zoospores may act as gametes (fig. 23, E), producing a spherical zygospore which becomes a new individual. As a matter of fact there appear to be no strong sexual tendencies in any of the simpler Chlorococcales, and it is well worthy of note in this connection that no case of oogamy and only one of anisogamy (*Phyllobium*) is reported from any member of the group.

In studying the life-history of species of *Chlorococcum*, formation of aplanospores (cf. p. 43) has often been observed, although it is not clear how readily this occurs in nature. These "arrested zoospores" are often formed in considerable numbers and it appears that the phenomenon may be repeated for more than one generation, with the development of palmelloid stages[1] whose cells may ultimately fall apart and resume the normal vegetative phase or be liberated as swarmers. In any case the aplanosporic state of *Chlorococcum* plainly shows the manner of evolution of such a form as *Chlorella* (fig. 23, A, B; 32), which appears as the starting-point of a whole series of Chlorococcales in which motility is apparently altogether suppressed. No detailed description of *Chlorella* is necessary at this point (cf. p. 118), suffice it to say that *C. vulgaris* Beyr. (fig. 23, A, B) is a replica of *Chlorococcum* developing new individuals straight away within the parent cells.

We owe to Oltmanns[2] and Brunnthaler[3] the clear recognition of these two types of unicellular Chlorococcales and of their interrelationship. Following the latter we may distinguish two main series, the Zoosporinae and the Autosporinae[4], of which *Chlorococcum* and *Chlorella* respectively represent the simplest known forms. It would however be incorrect to assume a common ancestry for all the forms grouped in these two series, since the Chlorococcales are almost certainly polyphyletic. A mere survey of the unicellular members suffices to make this clear; among the zoosporic forms we have *Trebouxia* (fig. 23, K)

[1] cf. Bristol, Journ. Linn. Soc., Bot. XLIV, 1920, p. 478.

[2] Oltmanns, Morph. u. Biol. d. Alg., first edit., 1904, p. 184.

[3] Verhandl. k. k. zool.-bot. Ges., Wien, 1913, p. 76.

[4] So called, because the daughter-individuals, both of the unicellular and colonial forms, usually acquire complete differentiation before they are liberated from the parent (cf. p. 44). Much the same thing occurs in the majority of the motile Volvocales.

with an axile massive lobed chloroplast, Gerneck's *Dictyococcus*[1] with numerous parietal lenticular chloroplasts, and the Chlorochytrieae with highly elaborated chloroplast-structure, whilst among the autosporic forms we have such an outstanding type as *Eremosphaera* (fig. 31). At the same time it is possible

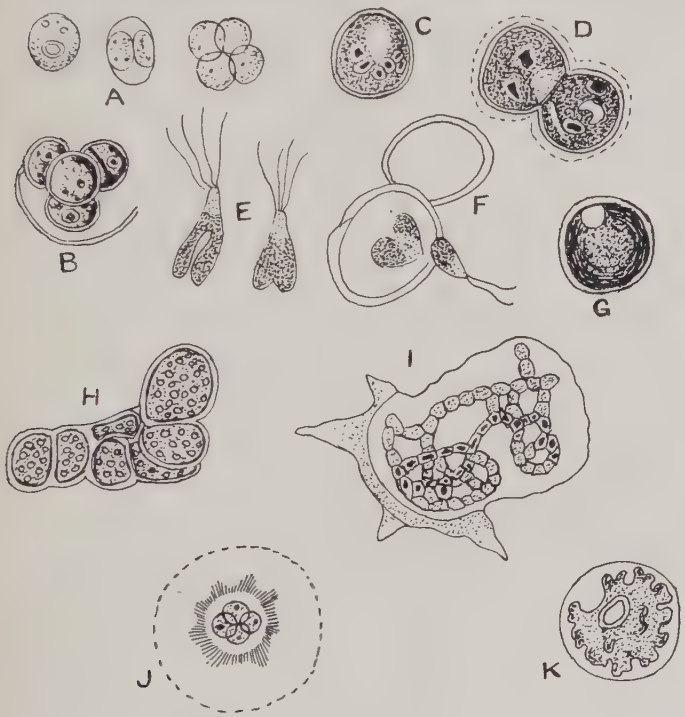

Fig. 23. A–B, *Chlorella vulgaris* Beijer.; A, three cells, the two on the right showing stages in division (after Chodat, × 800); B, liberation of daughter-cells (after Grintzesco, × 800). C–F, *Chlorococcum humicolum* (Naeg.) Rabenh. (after Bristol, E × 1435, the others × 825); E, fusion of swarmers; F, their liberation. G, *C. infusionum* Menegh. (after Artari, × 800). H, *Chlorosphaera consociata* Klebs (after Artari, × 440). I, Young *Hydrodictyon*-colony, arising within ruptured *Tetraëdron*-stage (after Pringsheim, × 300). J, *Radiococcus nimbatus* (De Wildem.) Schmidle (after De Wildeman, × 200). K, *Trebouxia humicola* (Treboux) (after Chodat).

that some of the unicellular and simpler colonial Chlorococcales are reduced from higher filamentous forms, but this is none too likely in view of the complete absence of vegetative division. This last should be clearly realised, since it forms perhaps the most marked connecting link between Chlorococcales and Volvo-

[1] Gerneck, 1907, p. 231.

cales. Nowhere in these two groups[1] is division of the cell by a simple septum to be encountered.

Many of the simpler Chlorococcales exhibit more or less pronounced saprophytic tendencies. Thus, *Chlorococcum infusionum* (Schrank) Menegh. favours stagnant waters rich in decaying matter, several species of *Chlorella* are capable of thriving in organic media (sewage, etc.)[2], sometimes with loss of chlorophyll, and others occur in the sappy exudations from various trees[3]. This tendency also finds its expression in the occurrence of species of *Chlorella* as symbiotic "green cells" within the bodies of various animals (*Paramoecium*, *Hydra*, freshwater sponges[4]), and in the occurrence of *Trebouxia* as the algal component of numerous Lichens (cf. p. 107). The same tendency may be responsible for the space-parasitism of *Chlorochytrium* (fig. 26, D) and *Phyllobium* (fig. 26, A).

Chlorochytrium is really nothing but a rather highly elaborated *Chlorococcum*, whose swarmers (sometimes zoospores, sometimes motile zygotes produced by the fusion of the swarmers) settle down on the surface of various higher aquatics (especially species of *Lemna*). After forming a membrane, a tubular prolongation grows into the "host," either through a stoma or between two epidermal cells, and swells out within one of the air-spaces. Here it forms a large cell which receives all the protoplasmic contents of the swarmer. This is the vegetative phase which lasts usually until the following season (fig. 26, D), when numerous zoospores are again formed and set free by rupture of the membrane and decay of the dead tissues of the host. In *Phyllobium* the germinating swarmer gives rise to a system of branching coenocytic tubes within the intercellular spaces of the host (leaves of *Lysimachia*, *Sphagnum* (fig. 26, A), etc.); at their ends large dark green swellings are formed (fig. 26, B), which show up conspicuously against the dead leaf-tissues and constitute the sporangia from which fresh swarmers are subsequently produced. This is obviously an advanced type, as shown also by the possession of anisogamous gametes, and points the way in which a line of fungal evolution might be initiated (cf. *Rhodochytrium*)[5].

[1] Except in *Chlorosphaera* (p. 107), which is very probably a reduced type.

[2] Beijerinck, Bot. Zeit. XLVIII, 1890, p. 730; Chick, Proc. Roy. Soc. London, LXXI, 1903, p. 458.

[3] cf. Krüger, in Zopf's Beitr. z. Physiol. u. Morph. IV, 1894, p. 91.

[4] Famintzin, Mém. Acad. Imp. Sci. St Pétersbourg, 7 sér. XXXVIII, 1891, No. 4; Brandt, Archiv f. Anat. u. Physiol., Physiol. Abt., 1882, p. 125; Beijerinck, loc. cit. p. 745; Limberger, Sitz.-Ber. Akad. Wien, CXXVII, 1918, p. 395.

[5] Lagerheim, Bot. Zeit. LI, 1893, p. 43.

Consideration of the remaining Chlorococcales resolves itself largely into a study of diverse types of colonies and coenobia which, except in *Hydrodictyon* (fig. 30), remain of microscopic dimensions and are mostly planktonic. In some of the simpler Autosporinae (e.g. *Radiococcus* (fig. 23, J); *Kirchneriella*, (fig. 43)) the small groups of cells are merely held together by a spherical or oblong envelope of secreted mucilage which may or may not be readily visible; similar colonies occur in a number of species of *Oocystis* (fig. 35, G), but here the mucilage-envelope appears to arise by the gelatinisation of the mother-cell membranes. Another simple method of colony-formation is seen in *Dactylococcus* (fig. 39) and *Selenastrum* (fig. 42) in which small groups of cells cohere at some point of their surface without any obvious mucilage-investment. In many species of *Ankistrodesmus* (fig. 40) the contact is so loose that the cells as often as not are found singly. In most of the forms so far mentioned the cells of the colony multiply by successive division of their protoplasts into usually four parts (cf. fig. 40, G, II; fig. 43, C) which, after acquiring membranes of their own, are liberated by the splitting or gelatinisation of the wall of the parent. A rather exceptional type of colony is seen in *Ankistrodesmus falcatus* var. *stipitatus*; here, after the membrane of the parent-cell has split open at one end, the daughter-cells shift to the aperture and becoming attached there form characteristic radiating tufts[1].

This helps towards the comprehension of the method of formation of the colonies in *Dictyosphaerium* (fig. 44) and *Dimorphococcus* (fig. 46), although as a general rule the cells are also held together by a common mucilage-envelope. The single cell from which such colonies originate, after undergoing the customary double division of its protoplast, shows splitting of the membrane into four equal or irregular pieces which remain cohering at one point. The daughter-cells cling to the tips of these segments which commonly roll up to form thread-like structures (fig. 44). As this process is repeated time after time, colonies of some size arise, all the cells of which are connected by branching threads.

The coenobial types are more highly specialised. In the Hydrodictyaceae division of the contents of a cell of the coenobium leads to the production of a number of biciliate zoospores (cf. fig. 28, G, J) which are never set free into the surrounding water, although passing out of the parent-cell into a delicate vesicle (fig. 28, G) in all except *Hydrodictyon*. In fact their move-

[1] cf. Chodat, 1902, fig. 89 (sub *A. Braunii*); Vischer, Rev. Hydrol. 1, 1920, p. 35, figs. 11–16. Similar colonies are met with in *Ophiocytium* (cf. p. 309).

ment is restricted to a slight quivering, lasting only for a short time. The cilia are very soon drawn in, the protoplasts assume the form and arrangement characteristic of the adult coenobium, and with the secretion of cell-membranes a new generation is initiated (cf. fig. 28, H; fig. 30, C). In the autosporic Coelastraceae (*Scenedesmus* (fig. 48); *Coelastrum* (fig. 49)) matters are essentially the same, but there is no zoosporic phase and the daughter-coenobia are immediately constituted from the products of successive division of the contents of a cell (fig. 49, D). In this family the individual cells of the coenobia are often held together by special mucilage pads or processes (cf. fig. 50, A). There is clearly not much difference between the coenobial types of the two series, as is well shown by the fact that suppression of cilia and of movement has been recorded for *Pediastrum*[1]. Moreover, *Sorastrum* (fig. 29), till recently regarded as one of the Coelastraceae, has now been shown to develop its daughter-coenobia as in the Hydrodictyaceae (cf. p. 115). The same fate may befall other Autosporinae, and here mention may be made of Massee's record of zoospores in *Dictyosphaerium*[2], an observation which, however, awaits confirmation.

As above mentioned, a large number of Chlorococcales are frequent in the plankton, and adaptations for this mode of life are seen in the development of plates (*Pediastrum* (fig. 28); *Crucigenia* (fig. 47, A–F)), needles (*Ankistrodesmus* (fig. 40); *Closteriopsis* (fig. 41, A)), and the frequent occurrence of wide mucilage-envelopes (*Kirchneriella*, (fig. 43)). Special developments in this sense are the elaborate nets of *Hydrodictyon*, and the various members of Chlorellaceae and Oocystaceae in which the cells are provided with more or less numerous and often elongate bristles, whereby the floating capacity is increased (*Micractinium* (fig. 34); *Chodatella* (fig. 37, G–I)). A mere glance at the figures of these forms suffices to show their close affinity with other types (*Chlorella*, *Oocystis*) not so equipped.

The near relationship of even the more specialised genera with the unicellular types is shown by the not uncommon production of isolated cells, scarcely distinguishable in shape or mode of reproduction from those of a *Chlorella*, in such forms as *Ankistrodesmus*, *Scenedesmus*, *Coelastrum*, etc.[3] The conditions that lead to this reversion to the unicellular state are not altogether clear. Both in *Ankistrodesmus*[4] and *Scenedesmus* (cf.

[1] West, 1916 *a*, p. 217.

[2] Massee, Journ. Linn. Soc., Bot. xxvii, 1891, p. 461.

[3] cf. Senn, Bot. Zeit. lvii, 1899, p. 40; Chodat, 1902, p. 163 et seq.; Chodat, 1913; Rayss, Mat. pour la Fl. Crypt. Suisse, v, 1915, Fasc. 2; Vischer, loc. cit.

[4] Vischer, loc. cit. p. 34, figs. 1–3.

p. 128) stages analogous to those presented by *Dactylococcus* are often seen; in fact one "species" of the latter (*D. infusionum* Naeg. (fig. 48, B)) is quite certainly merely a phase of the common *Scenedesmus obliquus* (Turp.) Kütz. and some algologists[1] would doubt the independence of *Dactylococcus* altogether.

Another indication of the close interrelation of the genera of Chlorococcales is furnished by the *Tetraëdron*-stages occurring in the life-cycles of *Hydrodictyon* (fig. 23, I) and *Pediastrum*, and more recently recorded also in *Oocystis submarina* Lagerh.[2] In the two first named they arise as the result of a sexual process. The gametes in these two genera are produced in the same way as the zoospores which they closely resemble; in this case, however, liberation into the surrounding water takes place and it is here that sexual fusion occurs with the formation of a spherical zygospore (fig. 28, K, L). The latter, after a period of rest, enlarges somewhat and its contents divide to form a small number of biciliate zoospores which swarm for a short time and then give rise to irregular cells, like those characteristic of the genus *Tetraëdron*. These slowly enlarge and ultimately a new *Hydrodictyon*-net or *Pediastrum*-plate is formed from the contents by the asexual method above described (fig. 23, I).

In *Oocystis*, as in all Autosporinae, there is no sexual process and the *Tetraëdron*-stages arise by a rejuvenescence of the protoplast of the ordinary cells. They represent resting-stages, from the contents of which the vegetative cells are subsequently produced. There can be no doubt, however, that there are also independent species of *Tetraëdron* reproducing again and again forms resembling themselves (fig. 38, A, B).

Following the arrangement proposed by Brunnthaler[3] (loc. cit.) the Chlorococcales are here classed in two series, viz.:

I. *Zoosporinae*, in which reproduction is effected by motile cells (zoospores or gametes).

II. *Autosporinae*, in which motile cells are absent and asexual reproduction is effected by means of aplanospores (autospores) which, before being set free from the parent individual, acquire all its characteristics; sexuality is not known to occur in this series.

Both series include unicellular and colonial or coenobial forms, which in the majority of cases are distinguishable from one another without reference to the mode of reproduction. The autosporic series is represented by a far greater diversity of forms—many of them specially adapted to a planktonic life—than the zoosporic one.

[1] Wille, 1909, p. 66.

[2] Wille, Ber. Deutsch. Bot. Ges. xxvi *a*, 1908, p. 816 et seq.

[3] cf. however Geitler, Arch. f. Protistenkunde, xlvii, 1924, p. 444, where a different system is advocated.

The following scheme should facilitate the identification of the British genera of Chlorococcales:

Series I. *Zoosporinae.*

A. Cells or coenocytes of varied form[1], free-living or endophytic *Chlorococcaceae*

a. Cells usually spherical[2], or more or less fusiform and epiphytic, but not endophytic in higher plants *Chlorococceae*

1. Cells approximately spherical, not epiphytic

* Cells never showing septation

† Chloroplast parietal, spherical, with an aperture on one side *Chlorococcum*

†† Chloroplast axile, massive, more or less lobed *Trebouxia*

** Cells occasionally showing septation, chloroplast spherical[3] *Chlorosphaera*

2. Cells commonly elongate, epiphytic *Characium*[4]

b. Cells or coenocytes of varied shape, usually as endophytes in higher plants, with elaborate chloroplasts *Chlorochytrieae*

1. Mature coenocytes with a thick wall, more or less rounded, free-living or more usually epi- or endophytic *Chlorochytrium*

2. Mature coenocytes forming a system of branching tubes, endophytic *Phyllobium*

B. Coenocyte, on damp mud, differentiated into a colourless subterranean rhizoid and a rounded green overground vesicle *Protosiphon* (*Protosiphonaceae*)

C. Coenobia composed of two or more cells, formed by apposition of zoospores, never completely liberated from the parent-cells *Hydrodictyaceae*

a. Coenobium a flat plate, microscopic

1. Coenobium two-celled *Euastropsis*

2. Coenobium of usually more than two, mostly of 32 or more cells *Pediastrum*

b. Coenobium spherical, microscopic, up to 64-celled, cells stalked, the stalks united at the centre *Sorastrum*

c. Coenobium of large coenocytes arranged in the form of a net, macroscopic *Hydrodictyon*

Series II. *Autosporinae.*

A. Unicellular, cells large, spherical, with numerous peripheral chloroplasts[5] *Eremosphaeraceae*

Only British genus *Eremosphaera*

[1] Cells often epiphytic, provided with sheathed or forked, often gelatinous bristles, see Chaetopeltidaceae (p. 204).

[2] Cells rod-shaped, sometimes cohering to form short filaments, see *Stichococcus* (p. 158).

[3] Cells usually dividing by transverse septa, chloroplast a parietal plate, see *Pleurococcus* (p. 209).

[4] cf. also *Characiopsis* (p. 308).

[5] If chloroplasts yellow-green and starch absent, cf. *Botrydiopsis* (p. 307).

B. Unicellular or colonial, cells usually globose, generally with an almost spherical chloroplast (except *Trochiscia*)
Chlorellaceae
a. Cells not provided with bristles *Chlorelleae*
1. Cells with a smooth membrane and a single chloroplast
* Cells usually single, or cohering in small groups, without a special mucilage-envelope *Chlorella*
** Cells arranged tetrahedrally within a special mucilage-envelope *Radiococcus*
2. Cells with a variously ornamented wall and sometimes several chloroplasts *Trochiscia*
b. Cells provided with long bristles, planktonic forms[1]
Golenkinieae
Only genus *Micractinium*

C. Unicellular or colonial, cells oblong or ellipsoid or (*Tetraëdron*) of very irregular shape, chloroplasts variable *Oocystaceae*
a. Cells oblong or ellipsoid, not provided with bristles
Oocysteae
1. Cells destitute of wing-like prolongations of the membrane
* Cells usually ellipsoid[2], often isolated, sometimes forming colonies *Oocystis*
** Cells often curved, oblong or ellipsoid, generally in small numbers within a mucilage-envelope *Nephrocytium*
2. Cell-membrane provided with a number of longitudinally arranged wings or ridges *Scotiella*
b. Cells more or less ellipsoid, with bristles *Lagerheimieae*
1. Bristles with a basal swelling *Lagerheimia*
2. Bristles without a swelling *Chodatella*
c. Cells of varied, usually angular shape, often with short spines
Tetraëdreae
Only genus *Tetraëdron*

D. Colonial, cells rarely solitary, of varied shape, but not globose, either held together by mucilage or cohering by parts of their surface *Selenastraceae*
a. Cells elongate, isolated or in small groups
1. Cells attenuated to acute apices, by which they are often connected to form loose colonies *Dactylococcus*
2. Cells more or less needle-shaped[3], of moderate length
* Cells isolated or in small loose aggregates, new individuals formed by transverse or crosswise division
Ankistrodesmus[4]
** Cells in parallel bundles of 2–8, enclosed by a mucilage-

[1] Cells often epiphytic, provided with sheathed or forked, often gelatinous bristles, see Chaetopeltidaceae (p. 204).
[2] If chloroplasts are blue-green, see *Glaucocystis* (p. 493).
[3] If septate, see *Raphidonema* (p. 190).
[4] cf. also *Elakatothrix* (p. 90).

envelope, new individuals formed by longitudinal division *Quadrigula*

3. Cells greatly elongated, attenuated into bristle-like points *Closteriopsis*

4. Cells ovoid, oblong, or club-shaped, often attached by their apices to form radiating colonies *Actinastrum*

b. Cells more or less lunate, colonial

1. Cells attenuated, arranged back to back to form small colonies without mucilage-envelope *Selenastrum*

2. Cells loosely and irregularly disposed within a wide mucilage-investment *Kirchneriella*

E. Colonial, cells spherical, oblong, or curved, connected by the often thread-like persistent walls of successive mother-cells into more or less compact colonies *Dictyosphaeriaceae*

a. Cells of a colony all of one shape

1. Cells indefinitely disposed, colonies spherical or ovoid

* Forked connecting threads well-marked, chloroplast parietal *Dictyosphaerium*

** Connecting threads indistinct, cells in radial series, chloroplast axile *Dictyocystis*

2. Cells grouped in fours in one plane, colonies irregular *Westella*

b. Cells in irregular colonies in groups of four, two of each group differently shaped to the other two *Dimorphococcus*

F. Coenobial, coenobia flat plates, rows, or spherical groups of cells, showing a very regular arrangement *Coelastraceae*

a. Coenobia flat, of variously shaped cells, with a mucilage-envelope

1. Coenobia of 4–32 cells in groups of fours, without marginal spines *Crucigenia*

2. Coenobia of four cells, with marginal spines or processes *Tetrastrum*

b. Coenobia usually of four or eight ellipsoid cells, united by mucilage-pads

1. Coenobia of four or eight cells, forming a single or double row, all in one plane *Scenedesmus*

2. Coenobia of four cells, ranged parallel to one another, in two planes *Tetradesmus*

c. Coenobia spherical, hollow, of 8–32 cells, united by special connecting pads *Coelastrum*

Series I. ZOOSPORINAE

Family 1. CHLOROCOCCACEAE

The forms comprised here are unicellular or coenocytic Algae, occurring in a great diversity of habitats and including an interesting series of "space-parasites." The chloroplast is usually

single and becomes very elaborate in the Chlorochytrieae; one or more pyrenoids are always present. Reproduction is normally effected by biciliate swarmers produced in considerable numbers by division of the protoplast. These act either as zoospores or gametes, in either case sooner or later coming to rest and initiating a new vegetative phase. The gametes are isogamous, except in *Phyllobium*, where anisogamy has been reported.

Sub-family 1. Chlorococceae

Cells usually spherical (except *Characium*), with a simple chloroplast, not endophytic.

Chlorococcum Fries, 1825[1] (incl. *Cystococcus* Naegeli, 1849). Cells spherical or, when massed to form a stratum, often angular as the result of mutual pressure, terrestr. or aquat. Chloropl. parietal, bell-shaped or almost completely spherical (cf. p. 95), usually with a median pyren. (several in older cells); membrane relatively thin; cells at first uni-, later multinucleate. Reprod. by biciliate zoosp. (8–32 per cell) or aplanospores; zoosp. sometimes acting as gametes. Akinetes with a thick wall and filled with orange-coloured oil also known.

The above diagnosis accords with the characteristics of Algae that have in recent years been usually referred to the genus *Chlorococcum*, although none of the details of cell-structure mentioned are recognisable in Fries's description. In using his generic name one is therefore appropriating to it a special sense which its author could hardly have intended. The first fairly satisfactory figure of a species of this genus is that of *C. infusionum* published by Meneghini in 1842[2]; although details are lacking, there can be no question but that the chloroplast is parietal and that it occupies practically the whole periphery of the cell. In 1849 Naegeli (loc. cit.) established another (terrestrial) species under the name of *Cystococcus humicola*; his figures are scarcely an improvement on Meneghini's, although the pyrenoid is recognised and additional details are given in the text. Since Meneghini's figure and description is prior to Naegeli's, the generic name *Chlorococcum* must have priority over *Cystococcus*. Brand (1925) uses the former name in a sense which is altogether unwarranted (cf. under *Trebouxia* below), whilst he wrongly adopts Naegeli's genus for the form here referred to *Chlorococcum* (cf. e.g. p. 304).

Only two sp. of *Chlorococcum* are certainly known to occur in Gt. Brit. Of these, *C. humicolum* (Naeg.) Rabenh. (*Cystococcus humicola* Naeg.; *Chlorosphaera limicola* Beij.) (fig. 23, C F) is a widely

[1] cf. Naegeli, 1849, p. 84 (sub *Cystococcus*); Artari, 1892, p. 11; Bristol, Journ. Linn. Soc., Bot. xliv, 1920, p. 473; Puymaly, Rev. Algol. i, 1924, p. 107.

[2] Meneghini, Monogr. Nostoch. ital., 1842, p. 27, t. ii, fig. 3.

distributed terrestrial form found in similar habitats to those frequented by the familiar *Pleurococcus* and often specially abundant on stone- and brick-work; it has also been obtained regularly from cultures of cultivated soils (Bristol, 1920, p. 75); cells usually 3–20 br., but sometimes much larger. *C. infusionum* (Schrank) Menegh. (*Chlorella infusionum* Beij.; cells 10–15 br., sometimes much larger) (fig. 23, G) is not uncommon in stagnant pools relatively rich in organic matter: the membrane is often rather thick and stratified.

Pleurococcus rufescens (Kütz.) Bréb. (cf. p. 212) is probably a species of *Chlorococcum*.

Trebouxia Puymaly, 1924[1] (*Cystococcus* of Treboux[2], Chodat[3], and other recent authors; *Chlorococcum* Brand, 1925). Cells spherical, with a thin wall, terrestr. Chloropl. axile, massive, more or less lobed, with a central pyren.; nucleus situated between two lobes of the chloropl. Reprod. similar to *Chlorococcum* (cf. below).

This Alga was first clearly distinguished from *Chlorococcum* by Treboux (loc. cit.), who applied to it the name *Cystococcus humicola* Naeg. The latter is however a species of *Chlorococcum* (cf. above), and there is no evidence that Naegeli's species included more than one form, although it is striking that he only observed aplanospores (cf. Puymaly, loc. cit. p. 110). Naegeli's *Cystococcus* being merged in *Chlorococcum*, a new name must be given to the Alga at present under discussion. *Trebouxia humicola* (Treboux) (*Cystococcus humicola* Treboux non Naegeli[4] (fig. 23, K)) is a common terrestrial form occurring in the same habitats as *Pleurococcus* and *Chlorococcum humicolum* and also found as a soil-Alga; it sometimes forms almost pure strata and is readily distinguished by its chloroplast from the other forms with which it is associated; the cells are 2–25 br., sometimes larger. Chodat (1913, p. 188 et seq.) has recorded zoospores, but aplanospore-development would appear to be more frequent.

Brand (1925, p. 328 et seq.) refers to the genus *Chlorococcum* two forms which are manifestly species of *Trebouxia* and regards the former genus as characterised by the possession of an axile chloroplast. The writer is of the opinion that there is no evidence in support of such a view. The identification with *Chlorococcum* is based on an assumed resemblance of a commonly occurring terrestrial Alga with axile chloroplasts (seemingly a form of *Trebouxia humicola*) with Greville's *Chlorococcum murorum*[5]. Neither Greville's figure, nor his description, however, admits of any conclusion as to the character of the chloroplast; moreover, his figure depicts elongate oval cells.

[1] Puymaly, loc. cit. p. 109.

[2] Ber. Deutsch. Bot. Ges. xxx, 1912, p. 69.

[3] Chodat, 1913, p. 186.

[4] Gerneck's *Cystococcus humicola* (= *Dictyococcus Gerneckii* Wille, 1909, p. 44) does not belong here.

[5] Greville, Scott. Crypt. Flora, vi, 1828, p. 325.

almost rod-shaped, one and a half to twice as long as broad, and more like a *Stichococcus* (p. 158) than anything else. As pointed out above, the first figure of a species of *Chlorococcum*, in which the character of the chloroplast can be recognised, leaves no doubt as to its parietal position.

Treboux (loc. cit.) first pointed out that *Trebouxia humicola* is the symbiont in the common Lichen *Xanthoria parietina*; the writer has examined *Parmelia physodes*, *P. caperata*, various species of *Cladonia*, and *Usnea floridana*, and in all cases finds that the green gonidia removed from the thallus of the Lichen possess all the characteristics of a *Trebouxia*. According to Chodat (loc. cit.) various species and physiological races are involved. Paulson and Hastings[1] however come to the conclusion that the Lichen gonidia belong to a species of *Chlorella*, but there is no evidence that the former ever have the parietal, almost spherical chloroplast of the latter genus. Paulson and Hastings also conclude that the distinct central body of the Lichen-gonidium is a nucleus, but all recent work on the cytology of the Chlorococcales has shown that the nucleus of the latter invariably possesses a distinct nucleolus and a clear nuclear membrane. Of this structure nothing is to be seen in the central body of the gonidium, which is certainly a pyrenoid. On the other hand, the body interpreted as the centrosome is quite clearly the nucleus, and the presence of several of such bodies in some of the cells shows that, as in *Chlorococcum*, nuclear division sets in some time before division of the protoplast takes place.

Chlorosphaera Klebs, 1883[2]. Cells with a thin wall, aquat., isolated or united to form flat or thread-like expanses, occasionally dividing by transverse septa. Chloropl. similar to that of *Chlorococcum*, but sometimes reticulate and commonly with several pyrens. Reprod. by biciliate zoosp. and akinetes. Probably a reduced type.

The most important point of distinction from *Chlorococcum* lies in the occasional occurrence of vegetative divisions, whereby irregular flat expanses or short filaments may be produced. No sp. of the genus is certainly recorded from the Brit. Isles, but thread-like expanses similar to those figured by Artari for *C. consociata* Klebs (fig. 23, H) have occasionally been encountered by the writer epiphytic on various submerged Phanerogams.

Characium A. Braun, 1849[3] (*Hydrocytium* A. Braun, 1855;

[1] Journ. Linn. Soc., Bot. XLIV, 1920, p. 502 et seq.; cf. also Paulson, Trans. Brit. Mycol. Soc. VII, 1921, p. 41, and Lorrain Smith, Lichens, Cambridge Bot. Handbooks, 1921, p. 56. I am indebted to Mr Paulson for allowing me to examine some of his preparations, and to Dr N. Carter for giving me the benefit of her considerable experience on algal cytology.

[2] cf. Artari, 1892, p. 35 et seq.

[3] Braun, 1855, p. 29; G. M. Smith, Ann. of Bot. XXX, 1916, p. 459; Carter, New Phytol. XVIII, 1919, p. 184.

Hydrianum Rabenhorst, 1868). Cells spherical or more commonly ellipsoid, oblong, or fusiform, generally asymmetrical, with a usually short stalk expanded into a basal disc, epiphytic on larger Algae or aquat. animals. Chloropl. parietal, often very indistinct (chlorophyll diffuse), with one or more pyrens. Reprod. by biciliate zoosp., often formed in considerable numbers (16–32) by progressive cleavage of the protoplast and liberated through a lateral or terminal aperture. *Palmella*-stages and akinetes also recorded.

Specific distinction[1] is based almost entirely on the form and size of the cells. Some ten sp. are known in Britain; of these the most

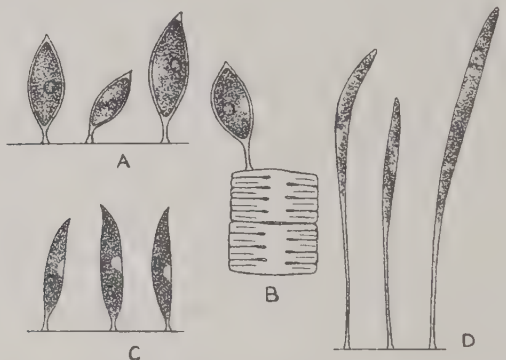

Fig. 24. A and B, *Characium Pringsheimii* A. Br.; A, from Mitcham Common, Surrey; B, attached to a frustule of *Tabellaria flocculosa*, from Gunwen Moor, Cornwall. C, *C. subulatum* A. Br., from Wimpole Park, Cambridgeshire. D, *C. Westianum* Printz, from Pilmoor, N. Yorks. (All ×520.)

general are *C. Sieboldii* A. Br. without a sharply demarcated stalk and with rather broad ellipsoidal cells (40–70 l.; 20–33 br.), *C. ambiguum* Herm. with curved lanceolate pointed cells (15–30 l.; 2·5–4 br.), *C. Pringsheimii* A. Br. (18–35 l.; 5–11·5 br.) (fig. 24, A and B), and *C. ornithocephalum* A. Br. with acuminate, asymmetric cells (19–33 l.; 8–12·5 br.) placed obliquely on the end of a relatively long stalk. *C. Westianum* Printz[2] (*C. ensiforme* West) (fig. 24, D) has very elongate cells (65–86 l.; 2·5–3·8 br.). *C. Debaryanum* (Reinsch) De Toni (*Dactylococcus Debaryanus* Reinsch), with broadly elliptical cells (12–18 l.; 7–9·5 br.), has been found epiphytic on *Cyclops* sp. in the Irish plankton.

[1] Species of this genus can be confused with germinating zoospores, especially of Chaetophorales. The absence of vegetative division and the customary presence of a stalk, however, make distinction easy.

[2] cf. Printz, Vidensk. Selsk. Skrift., No. 4, 1915, p. 17.

Sub-family 2. Chlorochytrieae

Cells or coenocytes of varied shape, with elaborate chloroplasts, often endophytic.

Chlorochytrium Cohn, 1874[1] (incl. *Endosphaera* Klebs, 1881; *Scotinosphaera* Klebs, 1881; *Centrosphaera* Borzi, 1883; *Stomatochytrium* Cunningham, 1888; *Chlorocystis* Reinhardt, 1885). Cells often endophytic in the intercell. sp. of various aquat. and marsh-plants (fig. 26, D), also in the soil, generally solitary, of varied shape (often ellipsoid or irregularly curved or lobed); cell-wall commonly thick and stratified, frequently with local excrescences. Chloropl. of a number of branches radiating out from a central mass and expanding at the periphery into broad parietal lobes or a complete parietal layer, usually with several scattered pyrens. Reprod. by biciliate swarmers formed in large

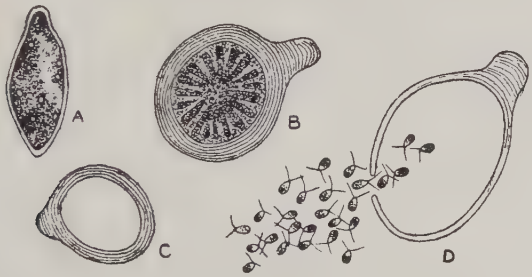

Fig. 25. A, vegetative cell of *Chlorochytrium Lemnae* Cohn, from Frizinghall, W. Yorks (×475). B–D, *C. Facciolaae* (Borzi) Bristol; B and C, from near Senens, Cornwall (×475); D, showing escape of zoospores (after Borzi, ×410).

numbers by successive div. of the protoplast and behaving either as zoosp. or gametes; aplanospores also observed. By thickening of the wall and storage of starch and oil the ordinary cells constitute resting-stages.

Of the four sp., so far known to occur in the Brit. Isles, the commonest is *C. Lemnae* Cohn (incl. *C. Knyanum* Cohn and Szymanski), often found in species of *Lemna* (fig. 25, A; fig. 26, C, D); the resting cells are 40–100 br. *C. paradoxum* (Klebs) G. S. West (*Scotinosphaera paradoxa* Klebs) has been found in a *Phormidium*-stratum growing in a soil-culture, although continental records show that it can also occur as an endophyte; the cells are 35–65 × 50–165, the membrane is often irregularly thickened, and the swarmers are formed from the contracted protoplast, the peripheral part of the cell-cavity being

[1] Klebs, Bot. Zeit. xxxix, 1881, p. 249; Bristol, Ann. of Bot. xxxi, 1917, p. 107; Bristol, Journ. Linn. Soc., Bot. xlv, 1920, p. 1.

filled with red granules. *C. Facciolae* (Borzi) Bristol (*Cystosphaera Facciolae* Borzi) has globose, shortly ellipsoid, or irregular vegetative cells (26–42 br.), which give rise to resting-cells (up to 80 μ br.) with peculiar localised projections of the thick membrane (fig. 25, B D); the cells usually occur in a diffuse stratum among the filaments of various Oscillatoriaceae.

The writer is on the whole in sympathy with G. S. West and Bristol as to the synonymy above given: doubt may be felt, however, in the case of *Endosphaera* where the mode of formation of the swarmers is

Fig. 26. A–B, *Phyllobium sphagnicolum* G. S. West (after G. S. West, ×250): A, edge of *Sphagnum*-leaf with a number of resting-cells attached to the vegetative threads; B, shows details of the chloroplast. C D, *Chlamydomyxum Lemnae* Cohn; C, section of resting-cell (after Bristol, ×720); D, small part of *Lemna* with resting-cells (after Klebs, × 200).

perhaps sufficiently distinctive to warrant a separate genus (cf. Klebs, loc. cit. p. 266). On the other hand, one may harbour a suspicion as to the independence of *C. paradoxum* and *C. Facciolae*.

Phyllobium Klebs, 1881[1]. Vegetative body composed of branched coenocytic threads, with or without septa, endophytic in or epiphytic on the leaves of marsh-plants. At certain points these threads swell up into elongate or globose thick-walled resting-cells, which receive all the protopl. contents and contain a complex chloropl., probably similar in type to that of

[1] Klebs, loc. cit. p. 268; West, 1908, p. 283.

Chlorochytrium; the resting-cells appear as bright green nodose swellings on the leaves of the "host." Within them are formed macrogametes, microgametes about one-third the size of the former, and zoosp., all biciliate, each resting-cell producing only one kind of swarmer. In sexual fusion the microgamete is completely engulfed by the macrogamete, so that the zygote is also biciliate; zoosp. and zygotes settle down upon the "host" or penetrate into it by way of a stoma.

P. dimorphum Klebs, which occurs usually in the dead leaves of *Ajuga*, *Lysimachia*, etc., forms its resting-cells along the principal veins; it has not yet been found in this country, although common on the continent. *P. sphagnicolum* G. S. West has been observed in the Hebrides and Achill Island in dead leaves of *Sphagnum*, which were studded with the dark green resting-cells (18–42 br.) arising from vegetative threads ramifying through the pores of the leaf-cells (fig. 26, A, B).

Family 2. PROTOSIPHONACEAE

This includes the single species *Protosiphon botryoides* (Kütz.) Klebs[1], which has so far not been found in this country. It frequents the damp mud round the edges of ponds and is usually intermingled with *Botrydium granulatum* (L.) Grev. with which, prior to Klebs's investigations, it was confused. The coenocyte is differentiated into a green spherical or elongate aerial portion and a long colourless rarely branched subterranean rhizoid. The centre of both regions is occupied by a continuous vacuole, the parietal cytoplasm harbouring numerous nuclei and, in the aerial portion, a reticulate chloroplast with many pyrenoids. On the approach of drought the cytoplasm breaks up into a number of cysts, often with a thick membrane and red contents. Reproduction is effected by biciliate swarmers formed in large numbers, either from the ordinary individuals or from the cysts; they may behave either as gametes or zoospores, in the former case producing thick-walled lobed zygospores which require a period of rest.

Family 3. HYDRODICTYACEAE

The members of this family possess coenobia composed of cells or coenocytes of very diverse form, but the similarity of the reproductive processes indicates their close affinity. New coenobia may be formed either asexually or sexually. In the former case biciliate zoospores arise by simultaneous or successive cleavage of the protoplast of one or more individuals of the coenobium.

[1] Klebs, 1896, p. 169.

In *Hydrodictyon* the zoospores remain confined within the parent-coenocyte and, according to Klebs, are permanently connected by delicate protoplasmic strands; in the other genera the mass of zoospores is liberated through a hole in the wall into a delicate vesicle, but they never swarm freely (fig. 28, G). In all cases the cilia are soon withdrawn and daughter-coenobia are formed, as the zoospores assume the form and arrangement typical of the particular genus (figs. 28, H; 30, E). Sexual reproduction, which has only been observed in *Hydrodictyon* and *Pediastrum*, involves the following steps: (*a*) production of biciliate isogametes which are liberated as separate swarmers (fig. 28, K) and fuse to form, (*b*) spherical zygospores (fig. 28, L) which after some time undergo gradual enlargement and give rise to, (*c*) a small number (2–5) of large biciliate zoospores which on coming to rest produce, (*d*) irregular *Tetraëdron*-stages which, after they

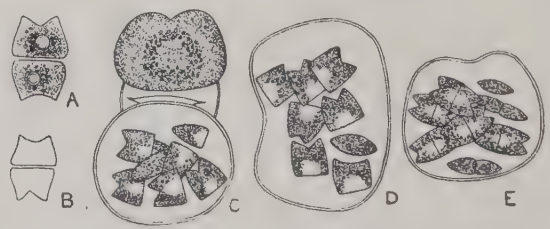

Fig. 27. *Euastropsis Richteri* (Schmidle) Lagerh. A and B, from near Senens, Cornwall (×760). C–E, showing formation of young coenobia (after Lagerheim; highly magnified).

have grown to a certain size, undergo division of their contents to form, (*e*) numerous zoospores of the usual type which, without swarming, reconstitute, (*f*) the normal coenobium in the way above described (fig. 23, I, p. 97).

The Hydrodictyaceae are a highly specialised group of Chlorococcales recalling in some respects the simpler coenobial Volvocales, although a direct connection is altogether improbable. Daughter-coenobia are formed in either case by apposition of motile cells, although motility is but a very brief phase in the Hydrodictyaceae. Moreover, in both cases separate swarmers are liberated in connection with sexual reproduction.

Euastropsis Lagerheim, 1894[1]. Coenobium of two flattened cells, joined along their straight inner margins, the outer margins widely notched, superficially resembling an *Euastrum*. Chloropl. a single parietal plate, with one pyren. Reprod. by oval biciliate zoosp., which swarm in a vesicle and then arrange them-

[1] Lagerheim, Tromsö Mus. Aarsheft. XVII, 1894, p. 12.

selves in pairs to form a number of new coenobia. Sexual process unknown. The development of several coenobia from one cell is really the only marked point of distinction from *Pediastrum*.

E. Richteri (Schmidle) Lagerh. (*Euastrum Richteri* Schmidle) (fig. 27) is only known in the Brit. Isles from bogs in Cornwall; coenobia 10–40 l.; 6–25 br.

Pediastrum Meyen, 1829[1]. Coenobium a free-floating flat plate, composed of a single layer (rarely double in the middle) of small coenocytes (4, 8, 16, 32, 64 in number)[2], which either have plane faces and are closely united or are lobed, so that perforations of variable size occur between them; marginal coenocytes usually of different shape to the central ones, generally with a pair of diverging processes, more rarely with a single one. Chloropl. in each coenocyte a parietal disc, later filling the whole, with 1–4 pyrens.; in cells of young coenobia there is only one nucleus, later several. Reprod. by biciliate zoosp., formed by successive nuclear div. followed by progressive cleavage of the protoplast and suddenly liberated into an external vesicle through a slit in the wall; here, after slight movement, they become arranged to form a new coenobium which acquires mature characteristics before liberation; complete suppression of cilia and of all movement is also recorded as a common phenomenon. Biciliate gametes, smaller than the zoosp., have been observed by Askenasy and fuse to form a smooth spherical zygosp.; the formation of large zoosp. from the latter (cf. *Hydrodictyon*) has not been seen, but *Tetraëdron*-stages giving rise to *Pediastrum*-plates are known. Formation of one or more hypnospores from the contents of the coenocytes has also been recorded[3] (fig. 28, E).

Specific distinction is mainly based on the form of the central and marginal coenocytes and on the characters of the membranes; the species, however, exhibit great variability in these respects and different authorities are not in agreement as to their limits. The natural habitat of sp. of *Pediastrum* is in small ponds and ditches amongst other water-plants, and they are not uncommon in quiet bog-pools.

[1] Ralfs, 1848, p. 180; Braun, 1855, p. 64; Askenasy, Ber. Deutsch. Bot. Ges. VI, 1888, p. 127; Heering, Mitteil. Altonaer Mus., 1904, p. 12; G. M. Smith, Ann. of Bot. XXX, 1916, p. 467; Harper, Mem. New York Bot. Gard. VI, 1916, p. 91; Harper, Proc. Amer. Phil. Soc. LVII, 1918, p. 375; Harper, Mem. Torrey Bot. Club, XVII, 1918, p. 210; Smith, 1920, p. 166; Chodat, 1922, p. 95.

[2] The coenocytes are often arranged in distinct rings round a central one, i.e. coenobium of $8=1+7$; coenobium of $16=1+5+10$; coenobium of $32=1+5+10+16$; but these arrangements are not always observed (cf. the papers of Harper just cited).

[3] Chodat and Huber, Bull. Soc. Bot. Suisse, v, 1895, p. 10.

They are sometimes abundant in the plankton. The tufts of rigid gelatinous bristles observed arising from the apices of the marginal processes and less abundantly from the surfaces of the central cells in some sp. (*P. Boryanum* (Turp.) Menegh., *P. clathratum* Lemm.) are no doubt an additional equipment for this mode of life; in *P. clathratum* and *P. simplex* they have been found to disappear during the winter[1].

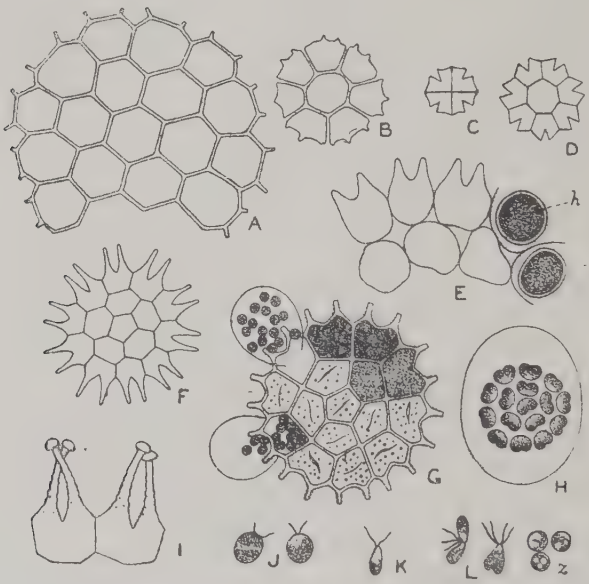

Fig. 28. A, *Pediastrum integrum* Naeg., from Ben Lawers, Perthshire (×475). B, *P. tricornutum* Borge, from Glen Tummel, Perthshire (×475). C and D, *P. tetras* (Ehrenb.) Ralfs, from Pilmoor, N. Yorks (×475). E, *P. duplex* Meyen, from Lough Fea, Londonderry, Ireland; hypnospores (*h*) (×475). F–H, *P. Boryanum* (Turp.) Menegh.; G, showing escape of zoospores; H, young coenobium formed by apposition of quiescent zoospores; F, from Frizinghall, W. Yorks, ×475; G and H, ×220 (after Kerner). I, two marginal cells of *P. glanduliferum* Benn., from Bisley Common, Surrey. J–L, *P. Boryanum* (after Askenasy); J, zoospores and K, gamete (×500); L, conjugation of gametes to form zygospores (*z*) (gametes ×730, zygospores ×220).

Of the eight Brit. sp., the two most abundant are *P. Boryanum* (Turp.) Menegh. (fig. 28, F–H and J–L) with extremely variable marginal processes and frequently granulate membranes, and *P. tetras* (Ehrenb.) Ralfs (*P. Ehrenbergii* A. Br.) (fig. 28, C and D) with coenobia of only four (diam. 10·5–18) or eight (diam. 22–29) cells; the plates of the former sometimes reach a diam. of 200 μ. Another

[1] Petersen, Bot. Tidsskr. xxxi, 1912, p. 166; also ibid. xxxvii, 1921, p. 199.

widely distributed sp. is *P. duplex* Meyen (*P. pertusum* Kütz.) (fig. 28, E) which likewise has bilobed marginal cells, but differs in the perforate character of the plate due to the lobed form of the central cells. *P. simplex* Meyen and *P. clathratum* Lemm. are rarer sp. with only a single process to the marginal cells, the former with compact, the latter with perforate plates. In the likewise rare *P. integrum* Naeg. (fig. 28, A) the marginal cells are entire. *P. Boryanum* and *P. duplex* are the most abundant sp. in the plankton.

Sorastrum Kützing, 1845[1] (*Selenosphaerium* Cohn, 1879). Coenobium globose, commonly of 16–64 (rarely 4 or 8) stalked cells, the stalks uniting in the centre to form a small facetted mucilage-sphere; cells broadly sublunate, reniform, or subtriangular, each outward extremity bearing two spines

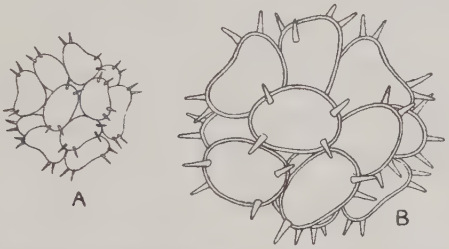

Fig. 29. *Sorastrum spinulosum* Naeg.: A, small coenobium from Pilmoor, N. Yorks (×475); B, large coenobium from Clifden, Galway, Ireland (×450).

(rarely one) of moderate length. Chloropl. parietal, with one pyren.; mature cells multinucleate. Reprod. by zoosp., which are liberated in a vesicle as in *Pediastrum* and there become grouped about a common centre, with the colourless anterior ends directed inwards; by these the stalks are secreted. Sexual reprod. unknown.

Of the two Brit. sp., that usually met with is *S. spinulosum* Naeg. (coenob. 31–90 br.; cells 11–26 l., without spines) (fig. 29); it is a rare form found in bog-pools or amongst aquatic Phanerogams in the quiet margins of lakes. In small coenobia the stalks of the cells are very short and the central sphere not always apparent. *S. americanum* (Bohlin) Schmidle occurs in the plankton of the Outer Hebrides: the heart-shaped or pyramidal cells are as long as broad.

Hydrodictyon Roth, 1800[2]. Coenobium forming a cylindrical

[1] Naegeli, 1849, p. 98; Bohlin, 1897, p. 40; Probst, Ber. Naturf. Ges. Baselland, 1916, p. 174; Geitler, Arch. f. Protistenkunde, XLVII, 1924 p. 440.

[2] Klebs, Flora, LXXIII, 1890, p. 351; Klebs, Bot. Zeit. XLIX, 1891, p. 789; Timberlake, Bot. Gaz. XXXI, 1901, p. 203; Timberlake, Trans. Wisconsin Ac. Sc. XIII, 1902, p. 486; Harper, Bull. Univ. Wisconsin, No. 207, 1908, p. 279.

sac-like network, reaching a length of 8–20 cm. and floating freely; meshes of the net of variable size, each bounded by five or six coenocytes, the angles being formed by the junction of three of the latter. Coenocytes elongate-cylindrical, with a large central vacuole and a lining layer of cytoplasm containing many nuclei; the nature of the chloropl. in the Brit. sp. is not clear, some describing it as reticulate, whilst according to Timberlake

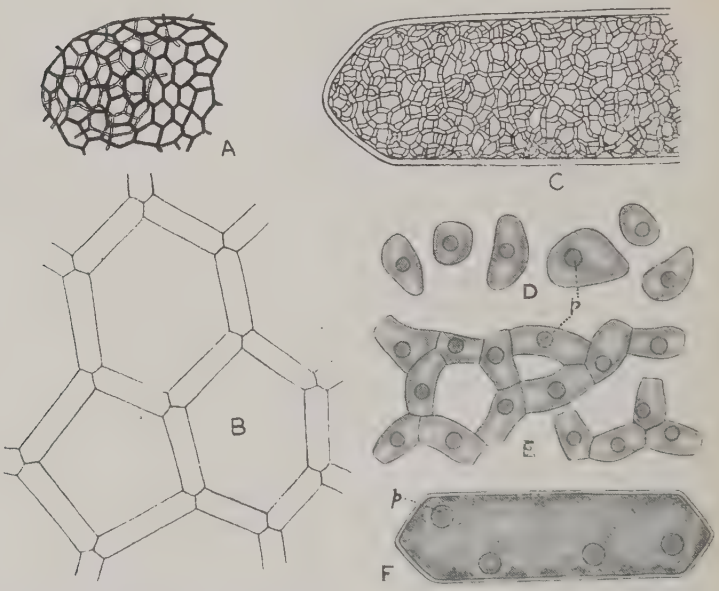

Fig. 30. *Hydrodictyon reticulatum* (L.) Lagerh., from the River Lea. A, nat. size; B, small portion of a young coenobium (×110); C, part of a large coenocyte containing a very young coenobium (×110); D, quiescent zoospores (×480); E, zoospores which are becoming apposed to form a new coenobium (×480), *p*, pyrenoid; F, slightly older coenocyte with four pyrenoids (*p*), ×480.

(loc. cit.) chlorophyll is diffusely distributed through the whole peripheral region[1]; pyrens. numerous. Reprod. by the formation of large numbers of biciliate uninucleate zoosp. by progressive irregular cleavage of the protoplast of a coenocyte; these, after swarming within it, come to rest and arrange themselves to form a new net. With reference to the sexual reprod. and the *Tetraëdron*-stages resulting from it, see pp. 101, 112.

[1] cf. also Smith, 1920, p. 165.

H. reticulatum (L.) Lagerh., popularly known as the "water-net," is a rare Brit. Alga (fig. 30), to which the above description especially applies: aver. length of adult coenocytes, 4–5 mm., but they may be 1 cm. long: length of quiescent zoosp. at the time of their apposition 13·5 -25 μ: swarming zoospores are 10 × 8 μ and the gametes a little smaller. A second interesting sp. is *H. africanum* Yamanouchi[1] which at present has only been found in South Africa; here the coenocytes composing the nets gradually enlarge to form huge spheres, 1 cm. or more in diam., which separate from one another prior to the formation within them of a new coenobium.

Series II. AUTOSPORINAE

Family 1. EREMOSPHAERACEAE

This family is essentially characterised by its large cells which contain numerous peripheral chloroplasts. Only one of the two known genera has been found in this country.

Eremosphaera De Bary, 1858[2] (*Chlorosphaera* Henfrey, 1859). Cells solitary, large, spherical, with a thin 2-layered membrane, aquat. Chloropl. numerous, small, parietal, or also

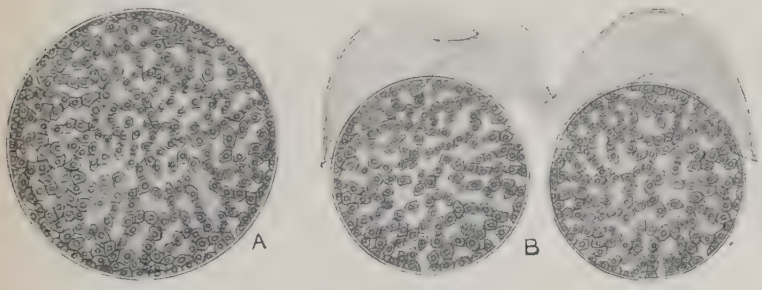

Fig. 31. *Eremosphaera viridis* De Bary, from near Clapham, W. Yorks (× 175).

in the cytoplasmic strands extending to the centre, of varying shape, each furnished with a conical projection directed towards the centre of the cell and each with 1–4 pyrens.; nucleus suspended in centre of cell. Multipl. by div. of the protoplast into two or four autospores liberated by the rupture of the parent cell-membrane; rejuvenescence of protoplast without div. also observed. Resting-spores with a thick wall and red oily contents recorded.

[1] Yamanouchi, Bot. Gaz. LV, 1913, p. 74.
[2] Moore, Bot. Gaz. XXXII, 1901, p. 309.

The polymorphism at one time ascribed by Chodat[1] to this Alga is discredited by Moore's investigations, as well as by G. S. West (1904, p. 229), who kept specimens under cultivation for two years without observing the development of other forms than the globular daughter-cells.

E. viridis De Bary, the only sp., is widely distributed over the Brit. Isles, more especially in *Sphagnum*-bogs; it is a constant associate of certain Desmids. The cells vary from 55–200 μ in breadth (fig. 31).

Family 2. CHLORELLACEAE

The members of this family are unicellular or colonial, the cells in most cases being globose with a typical "chlorococcoid" structure (p. 95). The colonies are of a simple type, the individuals merely adhering to one another or being held together by an envelope of mucilage. Reproduction is effected in the manner typical of the Autosporinae.

Sub-family 1. Chlorelleae

Cells not provided with bristles, rarely planktonic.

Chlorella Beijerinck, 1890[2] (incl. *Palmellococcus* Chodat, 1894). Cells small, globular, more rarely ellipsoid, commonly solitary or sometimes aggregated to form a thin mucous stratum, habitat very varied. Chloropl. single, parietal, resembling that of *Chlorococcum* or a curved plate, with or without a pyren.; cell-wall relatively thin. Reprod. by successive div. of the protoplast to form 2–8 (rarely as many as 64) new cells. Akinetes also recorded.

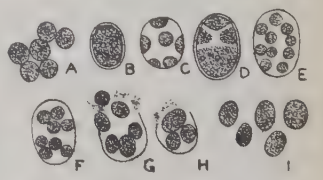

Fig. 32. *Chlorella miniata* (Kütz.) Wille, from near Bradford, W. Yorks (× 720).

The sp. of this genus are found in terrestrial situations, in media rich in organic matter (sewage waters, old cultures, etc.), in the sappy exudations of trees, and as "green cells" in symbiotic relationship with *Hydra viridis*, *Paramoecium*, *Ophrydium*, freshwater Sponges, etc.[3]

Three Brit. sp. are known. *C. vulgaris* Beij. (cells 5–10 br.) (fig. 23, A, B) is widely distributed and often abundant in cultures or in

[1] Chodat, Bot. Zeit. LIII, 1895, p. 137.

[2] Beijerinck, Bot. Zeit. XLVIII, 1890, p. 758; Chodat, Bull. Herb. Boissier, II, 1894, p. 599; Wille, 1909, p. 56; Chodat, 1913, p. 84 et seq.

[3] With reference to the reputed occurrence of species of *Chlorella* as Lichen-gonidia, see p. 107.

stagnant aquaria. It appears to grow as readily in the dark as in the light and can form chlorophyll in the dark[1]. *C. pyrenoidosa* Chick[2] (cells usually 3–5 br.), with a conspicuous pyren., is found in sewage-waters. *C. miniata* (Kütz.) Wille (*Palmellococcus miniatus* (Kütz.) Chod.; *Pleurococcus miniatus* Naeg.) (fig. 32) is not infrequent on walls or plant-pots in greenhouses, forming a moist brownish-green scum which often turns to an orange-red colour owing to the presence in the cells of a coloured oil obscuring the chloropl. which is devoid of a pyren.: cells 2–12·5 br. At times of drought the cells develop into orange- or red-coloured akinetes.

Aerosphaera Gerneck (1907, p. 251) is regarded by West and others as a section of *Chlorella* (West, 1916 *a*, p. 194: Wille, 1909, p. 56); here the chloropl. is reticulate and folded.

Minute green spherical cells (diam. 2 μ), with the general structure of a *Chlorella*, are occasionally met with in small pieces of water and in aquaria as a practically pure growth. Such would appear to belong to *Nannochloris coccoides* Naumann[3].

Radiococcus Schmidle, 1902[4] (*Westella* De Wildeman, 1897 (in part)). Cells grouped in small colonies, generally composed of four individuals arranged tetrahedrally and enveloped in a wide spherical mass of mucilage occasionally showing a radiate structure; cells rounded or angular by mutual pressure, with firm walls and "chlorococcoid" structure. Reprod. by formation of 4-celled colonies within each cell, whose membrane ruptures to set them free, its remnants persisting for some time at the periphery of the new colony.

There are four sp., of which *R. nimbatus* (De Wild.) Schmidle (*Pleurococcus nimbatus* De Wild.; *Tetracoccus nimbatus* Schmidle; *Westella nimbata* De Wild.) (fig. 23, J) is known from several parts of England, the colonies often occurring attached to the under surfaces of Water-Lily leaves; cells 8–15 br.

Trochiscia Kützing, 1845[5] (*Acanthococcus* Lagerheim, 1883; *Glochiococcus* De Toni, 1888). Cells globose, solitary, with a variously ornamented somewhat thickened wall, often occurring in large aggregates in quiet water or on damp ground; cell-wall either provided with a network of ridges or thickly clothed with denticulations or spines. Chloropl. probably single in young

[1] cf. Radais, Comptes Rendus, CXXX, 1900, p. 793; Grintzesco, Rev. gen. Bot. XV, 1903, p. 74.

[2] Chick, Proc. Roy. Soc. LXXI, 1903, p. 458.

[3] Arkiv f. Bot. XVI, 1919, No. 2, p. 18.

[4] Schmidle, Allgem. Bot. Zeitschr. VIII, 1902, p. 41 and Hedwigia, XLI, 1902, p. 159; cf. also De Wildeman, Bull. Herb. Boissier, V, 1897, p. 532.

[5] Reinsch, Ber. Deutsch. Bot. Ges. IV, 1886, p. 237; Hansgirg, Hedwigia, XXVII, 1888, p. 126; Wille, Videnskab. Selskab. Skrifter, Christiania, Mat.-nat. Kl., 1900, No. 6, p. 7.

cells and chlorococcoid, later (as a preparation for div.?) several, parietal, each with a single pyren. Reprod. probably solely by successive div. of the protoplast, the daughter-individuals acquiring their distinctive markings before or after liberation from the parent-cell; a *Palmella*-like state has been recorded in one sp.

A large number of the described "species" of *Trochiscia* are almost doubtless zygospores, etc. of various other Algae; a number are likely to be pollen grains or spores of higher plants. There are, however, a number of good species in which formation of new individuals resembling the parent has been observed. Wille[1] refuses to recognise the genus and regards most of the

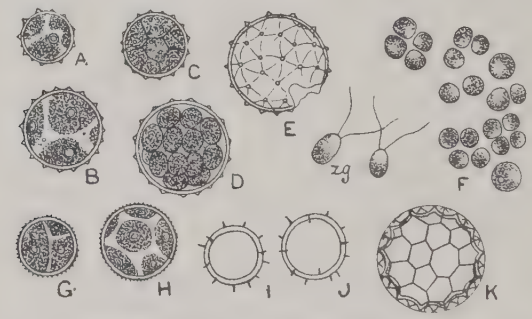

Fig. 33. A–F, *Trochiscia aspera* (Reinsch) Hansg., from Tremethick, Cornwall; A and B, vegetative cells; C and D, formation of new individuals; E, empty cell from which the latter have escaped (the zoospores *zg* in all probability do not belong here); F, palmelloid state. G and H, *T. hirta* (Reinsch) Hansg., from Cambridge. I and J, *T. paucispinosa* West, from Ben Lawers, Perthshire. K, *T. reticularis* (Reinsch) Hansg., from Keston Common, Kent. (All ×520.)

forms as zygospores of Chlamydomonadaceae, but this appears in no way justified, the more so as development of zoospores is highly doubtful. The swarmers shown in fig. 33 and referred to in the first edition of this work (West, 1904, p. 204) were practically disclaimed by its author at a later date (West, 1916*a*, p. 193), and Wille's data do not appear in any way conclusive. Nor is there any confirmatory evidence as to the reputed occasional occurrence of vegetative division.

Some eight or nine Brit. sp., distinguished by their external ornamentation, have been recorded, but all of these are not likely to be independent forms. The most frequent sp. encountered in quiet waters are: *T. aspera* (Reinsch) Hansg. (13·5–29 br.) (fig. 33, A–F), *T. aciculifera* (Lagerh.) Hansg. (up to 30 br.) with cells covered with

[1] Wille, loc. cit. p. 12.

numerous fine spines (up to 5 μ long), and *T. reticularis* (Reinsch) Hansg. (24–32 br.) (fig. 33, K). *T. aspera* is commonly found in and on soil, also but more rarely *T. hirta* (Reinsch) Hansg. (17–27 br.) (fig. 33, G and H), the latter especially near the base of tree-trunks.

Sub-family 2. Golenkinieae

Cells provided with bristles, planktonic.

Micractinium Fresenius, 1856[1] (incl. *Phytelios* Frenzel, 1891; *Golenkinia* Chodat, 1894; *Richteriella* Lemmermann, 1896). Cells spherical, solitary or in groups, with firm walls bearing a number of variously disposed solid or hollow bristles; cell-structure chlorococcoid. Reprod. by autospore-development; resting-spores with a thick membrane also known.

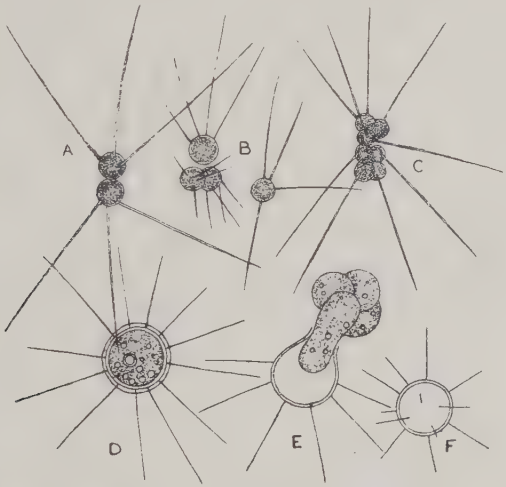

Fig. 34. A, *Micractinium pusillum* Fresen., after Lemmermann ($\times$ 520). B and C, *M. pusillum* forma *quadriseta* (Lemm.); B, from the plankton of Lough Beg, Ireland ($\times$ 450); C, after Lemmermann ($\times$ 520). D and E, *M. radiatum* (Chod.) Wille, after Chodat ($\times$ about 800). F, *M. paucispinosum* (W. & G. S. West), from the plankton of Lough Neagh, Ireland ($\times$ 450).

Three Brit. sp. are known, but none of them are common; they are found in the plankton of large lakes, but more commonly in ponds and canals. In *M. radiatum* (Chod.) Wille (*Golenkinia radiata* Chod.; cells 10–15 br., bristles 25–45 l.) (fig. 34, D and E) and *M. paucispinosum* (W. & G. S. West) (*G. paucispinosa* W. & G. S. West; cells 15–16 br., bristles 16 l.) (fig. 34, F) the cells are usually solitary, are

[1] Chodat, Journ. de Bot. VIII, 1894, p. 305; Lemmermann, Hedwigia, XXXVII, 1898, p. 304; Wille, 1909, p. 57.

enveloped by a thin layer of mucilage, and the evenly disposed bristles are solid. In *M. pusillum* Fresen. (*Richteriella botryoides* (Schmidle) Lemm.; cells 3–9·6 br.; bristles 23–60 l.) (fig. 34, A–C) the cells generally cohere to form loose colonies of 8, 16, 32, or 64 cells which bear hollow bristles attached only to those surfaces which face outwards.

Chodat has recorded quadriciliate zoosp. in *M. radiatum*, but this has never been confirmed[1].

Family 3. OOCYSTACEAE

The cells are usually oblong or ellipsoid (irregular in *Tetraëdron*), either solitary or forming small colonies enclosed in a distinct mucilage-envelope formed from the membrane of the parent-cell. The number and form of the chloroplasts are very variable. Reproduction takes place by typical autospore development.

Sub-family 1. Oocysteae

Cells oblong or ellipsoid, without bristles.

Oocystis Naegeli, 1845[2] (incl. *Oocystella* Lemmermann, 1903). Cells ellipsoid, subcylindrical, or panduriform, with a firm wall,

Fig. 35. A and B, *Oocystis solitaria* Wittr., from Ben Lawers, Perthshire. C and D, *O. crassa* Wittr.; C, from Lanlivery Moor, Cornwall; D, plankton form from Lough Beg, Ireland. E and F, *O. panduriformis* W. & G. S. West; E, from Pilmoor, N. Yorks; F, from near Clifden, Ireland. G, *O. elliptica* West, from Derryclare Lough, Galway, Ireland. (All ×485.)

[1] cf. also Chodat, 1902, p. 184.

[2] Chodat, 1897, p. 295; Wille, Ber. Deutsch. Bot. Ges. xxvi *a*, 1908, p. 812; Printz, Nyt Mag. f. Naturvidensk. li, 1913, p. 165; Smith, 1920, p. 110.

commonly provided with a nodular thickening at each pole, either solitary or in small groups within the gelatinised membrane of the parent-cell (sometimes enclosing several successive generations). Chloropl. parietal, one or more, usually several, discoid or stellate or reticulate, generally without pyrens. Reprod. by the development of 2–8 autospores per cell; resting-stages resembling a *Tetraëdron* are known in one sp. (cf. p. 101).

The sp. are distinguished by the form of the cell, the solitary or colonial habit, and the characters of the chloropl. There are about 12 Brit. sp., some of which are widely distributed in the quiet waters of ponds and lakes. *O. solitaria* Wittr. (cells 15–48 l.; 9·5–25 br.) (fig. 35, A and B), with usually solitary cells, is undoubtedly the commonest sp., although *O. elliptica* West (cells 24–25 l.; 11–11·5 br.) (fig. 35, G), which is usually colonial, is abundant. *O. parva* West, with cells having only 2–3 chloropl. and slightly pointed poles, is the smallest sp. (6–12 l.; 4–7 br.), and *O. gigas* Arch., with broadly elliptical cells having rounded ends, is the largest (41–50·5 l.; 32·5–40 br.). *O. crassa* Wittr. (14–26 l.; 10–20 br.) (fig. 35, C and D), whose chloropl. have pyrens., is only common in the plankton. *O. asymmetrica* W. & G. S. West is characterised by its asymmetrical and always solitary cells. In all of these sp., so far as they are known, the chloropl. are discoid, several per cell, and mostly without pyrens.; they belong to the section *Eu-Oocystis*. On the other hand, in *O. natans* (Lemm.) Wille (*Oocystella natans* Lemm.), which Bachmann (1907, p. 20) records from the plankton of Loch Leven, the chloropl. are stellately lobed and provided with pyrens.; this sp. belongs to the section *Oocystella*.

Nephrocytium Naegeli, 1849[1]. Cells oblong, ellipsoid, or subcylindrical, mostly slightly curved or sublunate, sometimes almost reniform, without any trace of polar thickenings, forming colonies of 2–16 cells placed peripherally within a usually well-defined mucilage-envelope. Chloropl. a large curved parietal plate with a pyren. Reprod. as in *Oocystis*, the daughter-cells remaining within the mucilage-envelope formed from the parent-membrane. The genus is not far removed from *Oocystis*, from which it is distinguished by the usually curved cells and the single chloropl.

There are four Brit. sp., of which *N. Agardhianum* Naeg. (incl. *N. Naegelii* Grun.), with kidney-shaped cells (12–22 l.; 7–12 br.), is widely distributed in the stagnant waters of small pools and lakes. *N. obesum* West is characterised by the short stout cells (34–42 l.; 24–28 br.) and the great thickness of the mature cell-wall (fig. 36, A). *N. lunatum* West (fig. 36, C–F), supposed by Chodat to be a stage of *N. Agardhianum*, is very local, but sometimes abundant among

[1] Naegeli, 1849, p. 79; Chodat, 1897, p. 298.

submerged *Sphagnum*; cells 14–18 l.; 4·6·5 br. *N. ecdysiscepanum* W. & G. S. West (fig. 36, B) is peculiar in that the walls of the parent-cells gradually throw off their outer layers, several generations being disposed in a fan-shaped manner and held in position by the partly exuviated strata; cells 24–26·5 l.; 13–17 br.

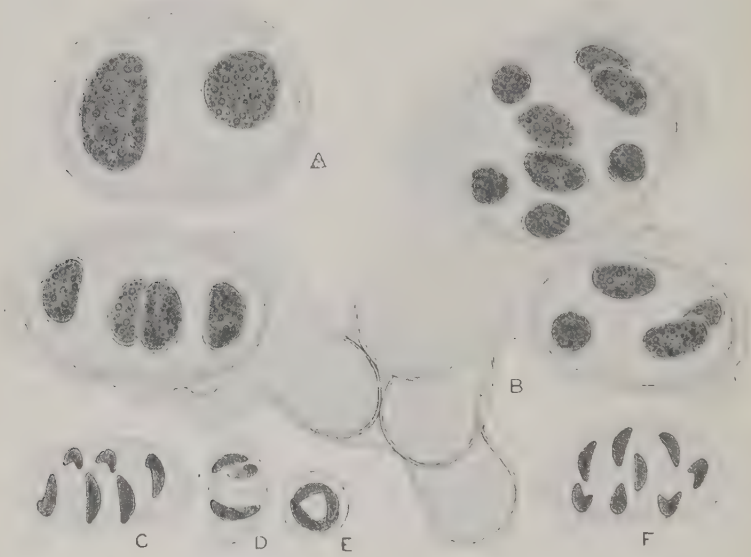

Fig. 36. A, *Nephrocytium obesum* West, from Angle Tarn, Cumberland. B, *N. ecdysiscepanum* W. & G. S. West, from near Goring, Oxfordshire. C–F, *N. lunatum* West; C–E, from near Bowness, Westmorland; F, from near Roundstone, Galway, Ireland. (All ×367.)

Scotiella Fritsch, 1911[1]. Cells solitary, ellipsoidal, with rounded or somewhat pointed poles, circular or elliptical in cross-section, with a number of regularly disposed longitudinal ridges or wings which may be somewhat sinuous. Chloropl. probably single, with a pyren.; fat often present. Reprod. uncertain, probably by formation of autospores, as in other Oocystaceae. Resting-cells also recorded.

This genus was first recorded as a member of the Yellow Snow flora from the Antarctic; other species have since been described by Chodat from Red Snow in the region of the St Bernard. The only Brit. record is a new sp., *S. Fritschii* B. M. Griff., found by Dr Griffiths in a pool occupying a rocky depression in Fallowfield Fell, near Hexham, Northumberland (cells 34–37 l.) (fig. 41, E–F).

[1] Fritsch, Journ. Linn. Soc., Bot. XL, 1911–12, p. 304; Chodat, 1922, p. 76.

Sub-family 2. LAGERHEIMIEAE

Cells more or less ellipsoid, provided with bristles.

Lagerheimia Chodat, 1895[1]. Cells usually solitary, ellipsoid or subcylindrical, with rounded ends and a firm wall bearing four symmetrically disposed bristles, with a wart-like thickening at the base of each. Chloropl. a parietal plate, generally with a small pyren. Reprod. by formation of 2–8 autospores which usually become free at maturity. Biciliate zoosp. recorded, but very doubtful.

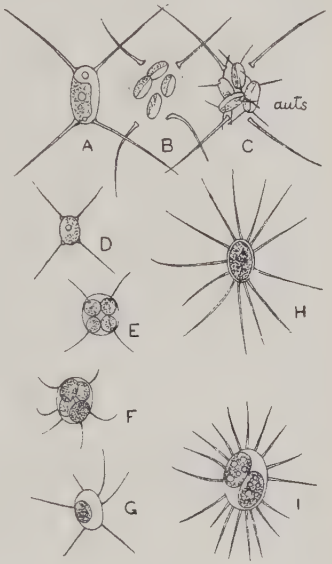

Fig. 37. A–C, *Lagerheimia genevensis* Chod., after Chodat (× about 850). D and E, *L. genevensis* var. *subglobosa* (Lemm.) Chod.; D, after Lemmermann (× 520); E, from Lough Gartan, Donegal, Ireland (× 450). F and G, *Chodatella breviseta* W. & G. S. West, from Lough Gartan, Ireland (× 450). H and I, *C. ciliata* (Lagerh.) Lemm. var. *amphitricha* (Lagerh.) Chod. (× 450); H, from Skipwith Common, E. Yorks; I, from near Bowness, Westmorland. *auts*, autospores.

Two sp. have so far been found in the Brit. Isles, both of them rare. In *L. genevensis* Chod. (cells 3–4·5 br.; 9–10 l.; bristles up to 16 l.) (fig. 37, A–C) and its var. *subglobosa* (Lemm.) Chod. (*L. subglobosa* Lemm.; cells 5·5–9·4 br.; bristles 10·5–13 l.) (fig. 37, D and E) the bristles are placed in pairs at the two extremities of the cells. In *L. Wratislaviensis* Schröd. (cells 8–9 br.; 11–12 l.; bristles 24–31 l.), however, there is one bristle at each end and one in the middle of each side. The sp. appear to favour a planktonic existence in pools and ponds.

Chodatella Lemmermann, 1898[2]. Cells solitary, ellipsoid, bearing four or many elongate bristles which are straight or curved and devoid of any thickening at the base. Chloropl. one or several, parietal, with or without pyrens. Reprod. as in *Lagerheimia*. It is doubtful whether this genus should be maintained, as the differences from *Lagerheimia* are very slight (cf. Wille, 1909, p. 58; West, 1916 *a*, p. 199).

[1] Chodat, Nuova Notarisia, VI, 1895, p. 86; Lemmermann, Hedwigia, XXXVII, 1898, p. 308; West, 1911, p. 85.

[2] Lemmermann, loc. cit. p. 309; West, 1908, p. 287.

Three sp. are recorded for this country, but they are all rare; they occur most frequently in the plankton of small pools, although also found in larger pieces of water. *C. ciliata* (Lagerh.) Lemm. (*Oocystis ciliata* Lagerh.; cells 12–21 l.; 9–18 br.) and its var. *amphitricha* (Lagerh.) Chod. (*C. radians* (West) Lemm.; cells 8–18 l.; 4–13·5 br.) (fig. 37, H and I) have cells bearing 12–18 bristles (12–20 μ long). In *C. breviseta* W. & G. S. West (cells 12–12·5 l.; 8–9·5 br.; bristles 11·5–17·5 l.) (fig. 37, F and G) there are six curved bristles. *C. quadriseta* Lemm. has only four bristles and approaches very close to a *Lagerheimia*.

Sub-family 3. Tetraëdreae

Cells of varied shape, commonly polyhedral, often bearing short spines.

Tetraëdron Kützing, 1845[1] (*Polyedrium* Naegeli, 1849; *Cerasterias* Reinsch, 1867). Cells solitary or rarely collected into temporary aggregates, flattened and angular (triangular, quadrangular, or polygonal) or polyhedral with obtuse or

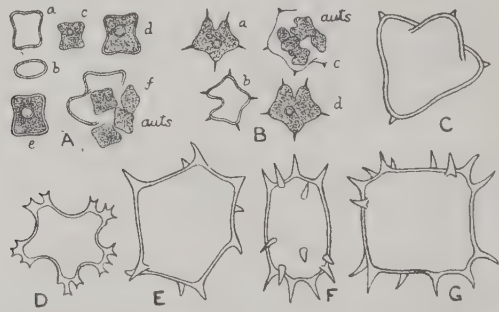

Fig. 38. A, *Tetraëdron minimum* (A. Br.) Hansg., from Keston Common, Kent. B, *T. caudatum* (Corda) Hansg., from Pilmoor, N. Yorks. C, *T. regulare* Kütz., from near Bowness, Westmorland. D, *T. enorme* (Ralfs) Hansg., from Mickle Fell, N. Yorks. E–G, *T. horridum* W. & G. S. West, from Putney Heath, Surrey. (All ×450.) *auts*, autospores.

acuminate angles, which may bear one or more simple or furcate spines; cell-wall smooth or granulate. Chloropl. one to many, parietal, with or without pyrens. Reprod. by the formation of 4–32 autospores, set free by the rupture of the wall of the parent, often into a delicate vesicle which soon disappears.

There are innumerable "species" of the genus, but only those can be regarded as certainly established in which reproduction by autospores is known to take place. *Tetraëdron*-like stages occur in the life-cycles of *Pediastrum*, *Hydrodictyon*, and *Oocystis*.

[1] Naegeli, 1849, p. 83; Reinsch, Notarisia, 1888, p. 493; West, 1908, p. 286; Smith, Ann. of Bot. xxxii, 1918, p. 459; Smith, 1920, p. 115.

Others of the described forms may be resting-stages of other Algae. The recording of such forms, even as new species of *Tetraëdron*, however, admits of their temporary classification until they can be assigned elsewhere.

There are about 16 sp. known to occur in the Brit. Isles, most of which favour small pieces of water; they rarely occur in considerable numbers. *T. minimum* (A. Br.) Hansg. is the most abundant of the flattened sp. (fig. 38, A); cells 6·5–16 br.; 5–7 thick. *T. regulare* Kütz. (*Polyedrium tetraëdricum* Naeg.) (fig. 38, C) is the commonest of the polyhedric sp.: cells 13·5–40 br. Other good sp. are: *T. caudatum* (Corda) Hansg. (fig. 38, B) and *T. muticum* (A. Br.) Hansg., the latter with triangular cells (12–30 br.). *T. enorme* (Ralfs) Hansg. (*Staurastrum enorme* Ralfs) (fig. 38, D) and *T. platyisthmum* (Arch.) G. S. West (*Cosmarium platyisthmum* Arch.) were originally described as Desmids.

According to Chodat[1] *T. enorme* should be transferred to the Heterokontae, since it lacks pyrens. and starch, has green or yellowish-green chloropl., and harbours fat. He establishes for it the genus *Pseudostaurastrum*, a name which can hardly be retained, since it has been used for a section of the genus *Tetraëdron*[2] to which other sp., as well as *T. enorme*, are referred (e.g. *T. horridum* W. & G. S. West (fig. 38, E–G)). The matter requires further investigation.

Reinsch's *Cerasterias* is distinguished from *Tetraëdron* proper by the depth of the lobing, the cells possessing 3–8 long arms with practically no central body. It is regarded as a section of *Tetraëdron* by Brunnthaler (1915, p. 158). Two sp., *T. rhapidioides* (Reinsch) Hansg. and the less robust *T. longispinum* (Perty) Hansg., are of rare occurrence in this country.

Brunnthaler (1915, p. 154) also includes *Reinschiella* De Toni, 1889 (*Closteridium* Reinsch, 1888) in the genus *Tetraëdron*, for which there is less warrant, since the cell-form is more like that of Selenastraceae. The cells are more or less curved (semilunar or semicircular), with simple spines at the apices, and closely resemble the cysts of certain freshwater Peridinieae (cf. p. 396); no doubt some of the species at least belong to that group. The only record for the Brit. Isles is *R. curvata* W. West (fig. 41, C) from Clare Island.

Family 4. SELENASTRACEAE

The cells vary in form, but are commonly needle-shaped or lunate, not globose. They are usually in loose colonies, the individuals of which are held together either by a mucilage-investment or by mere adhesion at certain points of their surface. Reproduction by autospore-formation.

[1] Bull. Soc. Bot. Genève, 2 sér. xii, 1920, p. 304.
[2] Brunnthaler, 1915, p. 154.

Dactylococcus Naegeli, 1849[1] (*Ourococcus* Grobèty, 1909; *Keratococcus* Pascher, 1915). Cells ellipsoidal, fusiform, pyriform, or sublunate, often asymmetrical and generally with acute apices, sometimes prolonged into spine-like processes, either solitary or loosely connected by their extremities to form fragile few-celled colonies; cell-wall thin, mucilaginous. Chloropl. single, parietal, with an often indistinct pyren., occasionally fragmenting into 2–4 pieces. Reprod. by oblique longit. div. of the protoplast with autospore-development.

Some sp. are truly aquatic, but most of them occur on wet rocks and moist surfaces, forming a dark green mucous stratum. *D. bicaudatus* A. Br. (*D. caudatus* Hansg.; cells 13–19 l.; 2·5–5·8 br.) (fig. 39, A) is a lunate sp., with apices greatly prolonged, inhabiting damp situations. The var. *subramosus* W. & G. S. West (fig. 39, B, C) forms

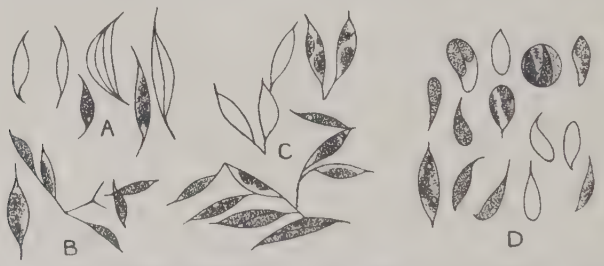

Fig. 39. A, *Dactylococcus bicaudatus* A. Br., from near Bradford, W. Yorks. B and C, *D. bicaudatus* var. *subramosus* W. & G. S. West, from Widdale Fell, N. Yorks. D, *D. dispar* W. & G. S. West, from Dorking, Surrey. (All ×520.)

characteristic colonies. *D. dispar* W. & G. S. West has unequally developed extremities and the cells are often of irregular shape (fig. 39, D). Both sp. have been encountered, though rarely, in cultivated soils.

D. infusionum Naeg. (fig. 48, B) is merely a stage in the life-history of *Scenedesmus obliquus* (Turp.) Kütz. It is usually aquatic and often occurs in immense quantity in the water in flower-pots and in aquaria. It exhibits great variability of form; cells 7·5–19 l.; 2·8–5·8 br. The genus *Dactylococcus* was originally founded by Naegeli for this form, but since its characteristics are shared by the other (probably independent) sp., there appear to be no grounds for the new name *Keratococcus* proposed by Pascher (1915, p. 216).

Ankistrodesmus Corda, 1838; emend. Ralfs, 1848[2] (*Rhaphidium* Kützing, 1845; *Schröderia* Lemmermann, 1898). Cells

[1] Naegeli, 1849, p. 85; Artari, 1892, p. 32; Grobéty, Bull. Soc. Bot. Genève, 2 sér. 1, 1909, p. 357; Chodat, 1913, p. 136.

[2] Corda, Almanach de Carlsbad, Prague, 1838, p. 196; Ralfs, 1848, p. 180.

fusiform with acute apices sometimes greatly produced and almost bristle-like, straight, curved, or sigmoid, generally many times longer than their diam., frequently solitary but more often variously grouped in loose aggregates; cell-wall very thin. Chloropl. single, parietal, occupying the greater part or the length of the cell, often without a pyren., but sometimes with one or two. Reprod. by autospores formed by oblique transv. and longit. div. of the protoplast into four, the products growing past one another till they assume a parallel arrangement and

Fig. 40. A, *Ankistrodesmus falcatus* (Corda) Ralfs, from Bewaise, Westmorland. B and C, *A. falcatus* var. *acicularis* (A. Br.): B, from Pilmoor, N. Yorks; C, from the plankton of Loch Mor Bharabhais, Lewis, Outer Hebrides. D, *A. falcatus* var. *tumidus* G. S. West, from Puttenham Common, Surrey. E, *A. falcatus* var. *mirabilis* G. S. West, from Wimbledon Common, Surrey. F, *A. setigerus* (Schrod.) G. S. West, from near Rievaulx Abbey, N. Yorks. G and H, *Quadrigula Pfitzeri* (Schröd.) G. M. Smith, from the plankton of Loch Mor Bharabhais, Lewis. (All × 520.) *auts*, autospores; *p*, pyrenoid.

usually attaining their full size before they are set free by gelatinisation or rupture of the membrane of the parent-cell.

Vischer[1] has studied *A. Braunii* (Naeg.) Collins in pure culture in diverse nutritive solutions and obtained a great range of forms, in part recalling other species and including *Chlorella*- and *Dactylococcus*-like stages; the normal cell is fusiform, about 4–7 times as long as broad, with pointed ends. Such experimental results, while of considerable interest as showing the plasticity of cell-form in the simple Algae, do not affect the specific limits until such stages have been shown actually to occur in a state of nature.

[1] Rev. Hydrol. 1, 1920, p. 5.

Sp. of *Ankistrodesmus* are widely distributed in all kinds of aquat. habitats, although most abundant in small ponds; a form of *A. falcatus* has been found as a rare constituent of the terrestrial algal flora (Bristol, 1920, p. 49). There are five Brit. sp., of which *A. falcatus* is very common: it possesses numerous varieties and the following synopsis will be found useful:

A. falcatus (Corda) Ralfs (*Rhaphidium fasciculatum* Kütz.; *R. polymorphum* Fresen. var. *falcatum* Rabenh.). Cells curved, 16–24 times as long as broad (1·5–3) with acute apices, in loose aggregates or close bundles, rarely solitary. Chloropl. usually without a pyren. (fig. 40, A).

Var. *acicularis* (A. Br.) G. S. West (*R. aciculare* A. Br.; *A. acutissimus* Arch.; *R. polymorphum* var. *aciculare* Rabenh.; *Closterium subtile* Bréb.). Cells usually solitary, straight or slightly curved, acutely attenuated, 36–65 (sometimes up to 165) l.; 2·5 3·5 br. Chloropl. sometimes with one or more pyrens. (fig. 40, B and C). G. S. West (1904, p. 223) was of the opinion that *R. pyrenogerum* Chod. belonged here, but it is now usually referred to *Closteriopsis longissima* Lemm.

Var. *duplex* (Kütz.) G. S. West (*R. duplex* Kütz.). Cells elongate, sigmoid, associated end to end in pairs.

Var. *tumidus* W. & G. S. West (*R. polymorphum* var. *tumidum* W. & G. S. West). Cells solitary or in small aggregates, curved and inflated in the middle, apices very acute, 61–73 l.; 4·5–6·5 br. Chloropl. with 1–2 pyrens. or none (fig. 40, D).

Var. *mirabilis* W. & G. S. West (*R. polymorphum* var. *mirabile* W. & G. S. West). Cells solitary, longer than in the type, variously curved, often sigmoid, apices very acute, up to 117 l.; 2–3·5 br. Chloropl. completely interrupted in middle of cell and often fragmented; vacuoles in protoplast often containing a single moving corpuscle (fig. 40, E).

Var. *spiralis* (Turn.) G. S. West (*R. spirale* Turn.; *R. fasciculatum* var. *spirale* Chod.). Cells in bundles of four or eight, twisted round each other in the central region of the cells, but free at their extremities, 32–45 l. Regarded as an independent sp. by Brunnthaler (1915, p. 190).

Var. *spirilliformis* G. S. West (*R. polymorphum* var. *spirale* W. & G. S. West). Cells always solitary, spirally twisted, making 1–1½ turns, apices very acute, 20–30 l.; often in prodigious quantity in stagnant water.

Other Brit. sp. are: *A. convolutus* Corda (*R. convolutum* Rabenh.) with short solitary cells, lunate or arcuate, only 3–6 times longer than broad (3–6) and with very acute apices: *A. setigerus* (Schröd.) G. S. West (*Reinschiella? setigera* Schröd.; *Schröderia setigera* Lemm.[1]; *R. setigerum* W. & G. S. West) with fusiform cells (5·7–6·5 br.; 75–88 l.) whose apices are attenuated into fine hair-like prolongations, chloropl. with one pyren. (fig. 40, F); and *A. Spirotaenia* G. S. West (1911, p. 86) distinguished by its very narrow cells, drawn out at the

[1] cf. Lemmermann, Hedwigia, xxxvii, 1898, p. 311.

apices into spine-like processes of great length (cells 171–185 l.; 2–2·1 br.), and by the spirally arranged chloropl.

Quadrigula Printz, 1915[1]. Cells cylindrical or fusiform, straight or slightly curved, with more or less acute apices, 8–10

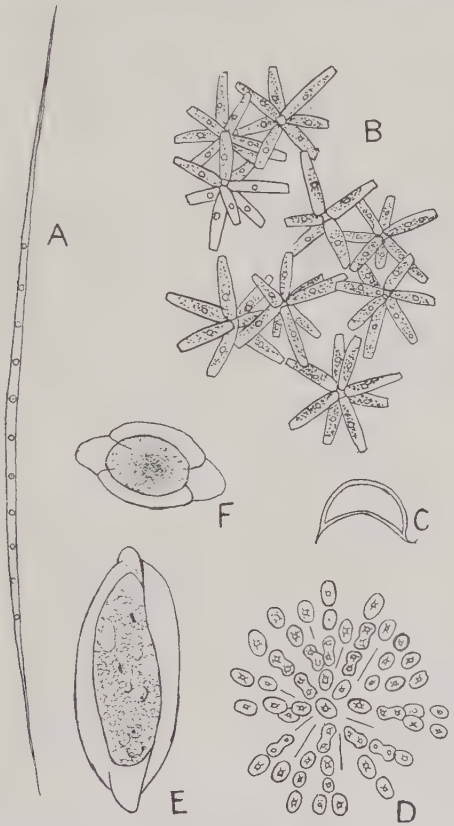

Fig. 41. A, *Closteriopsis longissima* Lemm. (after West). B, *Actinastrum Hantzschii* Lagerh. (after G. M. Smith, ×375). C, *Reinschiella curvata* W. West (after West, ×185), from Clare Island. D, *Dictyocystis Hitchcockii* (Wolle) Lagerh. (after Wolle, ×450). E–F, *Scotiella Fritschii* Griffiths (after drawings made by Miss Slee), from near Hexham, Northumberland (×1000); E, oblique lateral view; F, end view.

times as long as broad, generally in parallel groups of 2–8 within a hyaline mucilage-envelope. Chloropl. single, parietal, with or without pyrens. Reprod. usually by two simultaneous longit. divs. of the protoplast, with the formation of two or four (or eight)

[1] Printz, Videnskab. Selskab. Skrift., 1915, No. 2, p. 49.

autospores which remain lying parallel to one another within an envelope of secreted mucilage, the latter sometimes containing several generations.

This genus differs from *Ankistrodesmus* in the mode of div. of the protoplast and the consequent grouping of the new individuals. Printz (loc. cit. p. 50) suggests a reference to Oocystaceae which is perhaps justified. There is only one Brit. sp., *Q. Pfitzeri* (Schröd.) G. M. Smith (*Ankistrodesmus Pfitzeri* Schröd.) (fig. 40, G and H), which is not uncommon in the Scottish plankton; cells 38–49 l.; 7–8 br. Printz includes in this sp. *Nephrocytium closterioides* Bohlin (1897, p. 18).

Closteriopsis Lemmermann, 1898[1]. Differs from *Ankistrodesmus*[2] only in the great length of the cells and the 12 or more pyrens. in an axile series within the chloropl.; the ends of the cells are much attenuated into bristle-like points.

C. longissima Lemm., the only sp., is known from the plankton of Ireland and the Orkneys; cells up to 570 l.; 3·8–6 br. (fig. 41, A). In var. *tropicum* W. & G. S. West, recorded from the Shetlands, the ends are not setiform.

Actinastrum Lagerheim, 1882[3]. Cells ovoid, oblong, or club-shaped, 3–6 times as long as broad, generally cohering by their apices to form small radiating free-floating colonies. Chloropl. parietal, with a pyren. Reprod. by longit. or crosswise div. of the protoplast, usually into eight; the products, set free by rupture of the wall, diverge outwards but cohere by means of mucilage at their proximal ends; by repeated div. in the daughter-cells colonies of some size are sometimes formed.

The only Brit. sp. is *A. Hantzschii* Lagerh., which is very rare and mostly planktonic; cells 10–24 l.; 3–6 br. (fig. 41, B).

Selenastrum Reinsch, 1867[4]. Cells arcuate or lunate, attenuated to fine points and arranged with the convex surfaces apposed to form 4- or 8-celled colonies without a mucilage-envelope; cell-wall thin and firm. Chloropl.

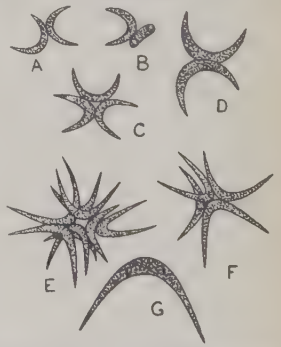

Fig. 42. A–D, *Selenastrum gracile* Reinsch; A–C, from near Settle, W. Yorks; D, from Puttenham Common, Surrey. E–G, *S. Westii* F. E. Fritsch, from Bowness, Westmorland. (All ×520.)

[1] Lemmermann, Forschungsber. Biol. Stat. Plön, VII, 1899, p. 124; West and West, 1906, p. 106.

[2] To which it is referred by Wille (1909, p. 68) and Brunnthaler (1915, p. 191).

[3] Lagerheim, Öfvers. K. Sv. Vet.-Akad. Förhandl., 1882, No. 2, p. 70.

[4] Reinsch, Algenfl. d. mittl. Theil. v. Franken, 1867, p. 64; Viret, Bull. Herb. Boissier, v, 1905, p. 706; Smith, 1920, p. 132.

parietal, without a pyren. Reprod. by autospores formed by transv. div. of the protoplast.

The three Brit. sp. are very uncommon, usually occurring amongst other water-plants at the margins of ponds and lakes. They are: *S. gracile* Reinsch (cells 19–28 l.; 4–5 br.) (fig. 42, A–D), *S. Bibraianum* Reinsch with more robust cells (16–23 l.; 5–8 br.), and *S. Westii* F. E. Fritsch (*S. acuminatum* G. S. West non Lagerheim[1]) (fig. 42, E–G).

Kirchneriella Schmidle, 1893[2] (incl. *Selenoderma* Bohlin, 1897). Chiefly differs from *Selenastrum* in the loosely aggregated

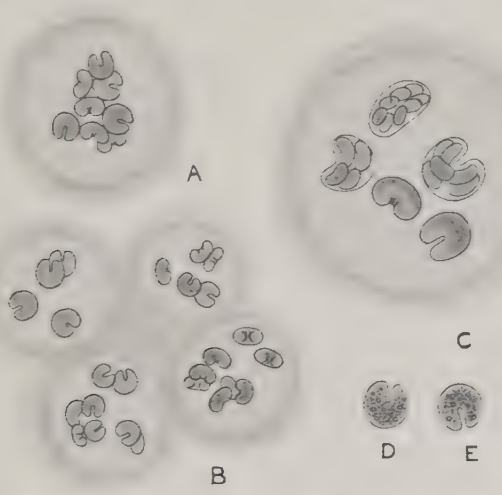

Fig. 43. *Kirchneriella obesa* (West) Schmidle. A, B, D, and E, from Bowness, Westmorland; C, from the plankton of Loch Mor Bharabhais, Lewis, Outer Hebrides (×485).

colonies composed of irregularly disposed cells, usually within a wide mucilage-envelope (reaching 500 μ in diam.). Cells arcuate or crescent-shaped, attenuated or subcylindrical, often bent until the apices almost meet; cell-wall very thin. Chloropl. parietal, on the convex wall of the cell, with or without a pyren. Reprod. by successive transv. or crosswise div. of the protoplast into four, the autospores remaining enclosed within the membrane of the parent or more usually being set free by its rupture.

Of the three Brit. sp., *K. obesa* (West) Schmidle (fig. 43; greatest diam. of cells 6–16; br. of cells 2–9·5; apices 1·5–4 apart) and *K. lunaris*

[1] cf. West, Journ. of Bot., 1912, p. 88. *S. acuminatum* Lagerh. is a species of *Scenedesmus*; see Fritsch, 1918, p. 507.

[2] Schmidle, Ber. naturf. Ges. Freiburg i. Br. VII, 1893, p. 82; Chodat, Bull. Herb. Boissier, III, 1895, p. 308; West, 1908, p. 284; Smith, 1920, p. 140.

(Kirchn.) Moeb., with semilunar or sickle-shaped cells with pointed ends, are abundant in the plankton of the larger lakes, though occurring only sparingly in smaller pieces of water. In *K. subsolitaria* G. S. West there is no mucilage-envelope, the daughter-cells remaining enclosed in the membrane of the parent-cell for some little time before liberation.

Family 5. DICTYOSPHAERIACEAE

The members of this family are distinguished by the fact that the 4 cells, usually resulting from the division of a parent-cell, remain adhering to the tips of the 4 (often thread-like) lobes into which the membrane splits. Since this occurs in several successive generations, more or less compact colonies composed of 4-celled coenobia result; mucilage is sometimes also secreted forming a usually inconspicuous envelope around the whole colony. The component cells are spherical, oblong, or curved, and each has a single chloroplast. Multiplication takes place by dissociation of the colonies.

Fig. 44. *Dictyosphaerium pulchellum* Wood. A, from the plankton of Loch Shin, Sutherland; B, from Cam Fell, W. Yorks (×450).

Dictyosphaerium Naegeli, 1849[1]. Cells globose, ovoid, or subreniform, with a firm wall, connected by forked threads (remnants of mother-cell membranes) to form roughly spherical or ellipsoid colonies, although large ones often become very irregular; entire colony enveloped in mucus, the cells being situated somewhat far apart towards its periphery. Chloropl. chlorococcoid. Enlargement of colony as described above; multipl. by dissociation. The biciliate zoosp. reported by Zopf and Massee require confirmation (cf. p. 100).

Three Brit. sp. are known, of which *D. Ehrenbergianum* Naeg.[2] is widely distributed, often occurring in quantity in the surface waters of ponds and in the plankton of lakes; its ovoid or ellipsoid cells are 6 10 l. and 4 7 br. *D. pulchellum* Wood (fig. 44) with spherical cells and *D. reniforme* Bulnh. with kidney-shaped cells are more rarely found.

[1] Naegeli, 1849, p. 72; Zopf, Beitr. z. Physiol. u. Morphol. nied. Organismen, Heft 3, 1893, p. 15; Francé, Österr. Bot. Zeitschr. xliii, 1893, p. 251; Borzi, Ber. Deutsch. Bot. Ges. xii, 1894, p. 248.

[2] The figure of this species given by Brunnthaler (1915, p. 184) is not typical and is more like *D. pulchellum*.

Dictyocystis Lagerheim, 1890[1]. Chiefly distinguished from *Dictyosphaerium* by the presence of an axile stellate chloropl. with a pyren. and by the arrangement of the oblong or ellipsoid cells in radiating series which frequently branch. The mode of development of the colony and the exact nature of the delicate threads which hold the cells in place require investigation.

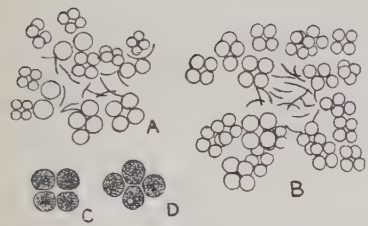

Fig. 45. *Westella botryoides* De Wildem., from Bowness, Westmorland. A and B, ×450; C and D, two "tetrads," ×715.

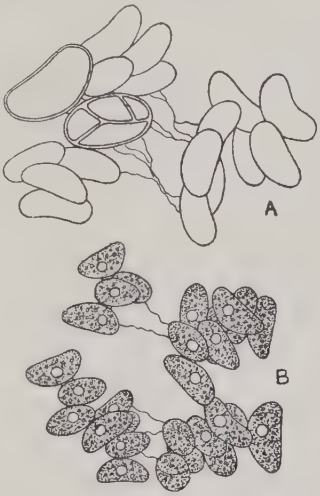

Fig. 46. *Dimorphococcus lunatus* A. Br.; A, from the plankton of Loch Mor Bharabhais, Lewis, Outer Hebrides; B, from Bowness, Westmorland (× 520).

D. Hitchcockii (Wolle) Lagerh. (*Dictyosphaerium Hitchcockii* Wolle) (fig. 41, D), the only sp., is a rare Brit. Alga occurring in the bogs of N. Ireland and N. W. Scotland and also in the Scottish plankton; cells 9–11 br. (the American specimens are larger).

Westella De Wildeman, 1897 (in part)[2] (*Tetracoccus* W. West, 1892)[3]. Cells small, globose or subglobose, sometimes a little angular, closely arranged in groups of four in one plane, the groups being connected by the delicate thread-like remnants of

[1] Lagerheim, Nuova Notarisia, I, 1890, p. 226. West (1916 *a*, p. 191) and Wille (1909, p. 28) include this genus in *Dictyosphaerium*, but the differences warrant generic separation. It is possible that *Dictyocystis* is really a *Cosmocladium* (Smith, Bull. Univ. Wisconsin, No. 57, Pt. II, 1924, p. 39).

[2] De Wildeman, Bull. Herb. Boissier, V, 1897, p. 532.

[3] W. West, Journ. Roy. Micr. Soc., 1892, p. 735; cf. also West, 1916 *a*, p. 191. The amended description given by Schmidle (Flora, LXXVIII, 1894, p. 47) is not correct, as the plant he included in it is not a species of *Westella*, but belongs to *Radiococcus*.

old mother-cell walls to form small free-floating colonies (with a max. number of 80 cells), practically free from enveloping mucus. Chloropl. bell-shaped with several large granules, but presence of pyrens. doubtful. Enlargement of colony by div. of protoplasts along two directions in one plane.

The only Brit. sp., *W. botryoides* De Wildem. (*Tetracoccus botryoides* W. West) (fig. 45), is widely distributed, generally occurring in the surface waters of ponds and in the plankton of large lakes: cells 3·8–5·7 br.; colonies 30–57 br.

Dimorphococcus A. Braun, 1849[1]. Cells arranged in composite colonies consisting of irregular agglomerations of definite groups of four cells disposed obliquely in one plane, the two central cells of each group being ellipsoid or oblong and the two outer ones cordate or reniform; the four cells of a group are held in position by irregular fragments of the mother-cell wall and the different groups represent successive generations held together in the same way; usually very little enveloping mucus. Chloropl. parietal, with pyren. Enlargement of the colony much as in *Dictyosphaerium*; when a certain size is reached, fragmentation into smaller colonies ensues.

D. lunatus A. Br. (fig. 46) is a rare Alga which sometimes occurs in the plankton, but is more often met with in the small tarns of mountainous districts; colonies 57–86 br.; cells 11–25 l.

Family 6. COELASTRACEAE

This family includes the typically coenobial members of the Autosporinae and is thus parallel to the Hydrodictyaceae among Zoosporinae. The coenobia assume varied forms, but the component cells are in almost all cases joined together by mucilage-pads or by processes of other kinds developed at certain points of their surface; in addition there is sometimes a mucilage-envelope, which is rarely visible without special staining. Reproduction is effected by the formation of a new coenobium within each cell of the parent.

Crucigenia Morren, 1830[2] (*Staurogenia* Kützing, 1849; *Lemmermannia* Chodat, 1899[3]; *Willea* Schmidle, 1900; *Cruci-*

[1] Braun, 1855, p. 44; Bohlin, 1897, p. 25; Crow, Ann. of Bot. xxxvii, 1923, p. 141.

[2] Morren, Ann. sci. nat. xx, 1830, p. 415; Schmidle, Ber. Deutsch. Bot. Ges. xviii, 1900, p. 149 (sub *Staurogenia*); Wille, Nyt Mag. f. Naturvidensk., xxxviii, 1900, p. 10; Smith, 1920, p. 144.

[3] *Lemmermannia* (Chodat, Mem. Herb. Boissier, No. 17, 1900, p. 5; Chodat, 1902, p. 221) differs essentially from *Crucigenia* only in the absence of a pyrenoid.

geniella Lemmermann, 1900). Coenobia composed of four cells of diverse shape arranged to form a flat or slightly curved plate, the cells being closely adherent except in the centre, where there is usually a small quadrate or rhomboidal space; daughter-coenobia generally combined to form larger plates, which are held together by a more or less conspicuous mucilage-envelope formed from the mother-cell membranes, this tendency not uncommonly extending to more than one generation, so that syncoenobia of 8, 16, 32, etc. (up to 128) cells may originate. Chloropl. cup-shaped, with or without a pyren.; cell-wall smooth. New coenobia are formed by crosswise div. of the protoplasts of the cells of the parent; multipl. takes place by dissociation of the syncoenobia. Resting-spores have been recorded in *C. rectangularis* (Naeg.) Gay.

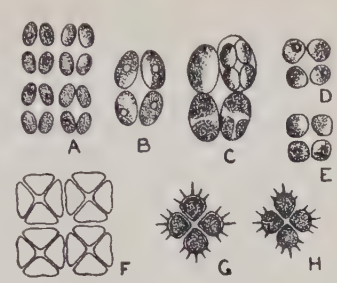

Fig. 47. A–C, *Crucigenia rectangularis* (Naeg.) Gay, from Lough Shannacloontippen, Galway, Ireland; C, with formation of autocoenobia. D and E, *C. quadrata* Morren, from Settle, W. Yorks. F, *C. Tetrapedia* (Kirchn.) W. & G. S. West, from plankton of L. Neagh, Ireland. G and H, *Tetrastrum Staurogeniaeforme* (Schröd.) Chod., from near Rievaulx Abbey, N. Yorks. (All ×520.)

In the frequent occurrence of syncoenobia this genus approaches the Dictyosphaeriaceae.

Specific distinction is essentially based on the form of the cells. All the sp. are constituents of the freshwater plankton. Of the six Brit. sp., *C. rectangularis* (Naeg.) Gay (cells 5–9 l.; 4–6 br.) (fig. 47, A–C) is the most frequent. *C. quadrata* Morren (=? *C. triangularis* Chod.) (fig. 47, D and E), distinguished by its rounded cells (5–5·5 br.), is much rarer. *C. Tetrapedia* (Kirchn.) W. & G. S. West (1902, p. 62) (*Tetrapedia emarginata* Schröd.; *Lemmermannia emarginata* Chod.) (fig. 47, F) is only known from the plankton of Lough Neagh and of a pool in the Midlands (Griffiths, 1922, p. 9); it is easily recognised by the shape of the cells (4·8–9·5 br.); the 4-celled coenobia are 10·5–15·5 in diam. The very small *C. minima* (Fitschen) Brunnth., with ovoid cells (3–3·5 br.), has so far only once been recorded (Griffiths, 1922, p. 10).

C. irregularis Wille, known from the plankton of several lochs in the Shetlands and from Norway, differs only in the somewhat irregular colonies and the absence of pyrens. from *C. rectangularis*, of which Brunnthaler (1915, p. 171) regards it as but a variety. The genus *Willea*, created for this sp. owing to the lack of pyrens. (Schmidle, loc. cit. p. 157), is no longer maintained, since little systematic value can be attached to such a feature.

Tetrastrum Chodat, 1895[1] (*Cohniella* Schröder, 1897). Differs from *Crucigenia* only in the presence of spines (rarely knobs) on the outer surfaces of the cells of the 4-celled coenobia and in the infrequent occurrence of syncoenobia; the mucilage-envelope is usually inconspicuous. The genus is thus artificial and its maintenance is purely a matter of convenience.

The three sp. recorded from the Brit. Isles are all very rare. *T. Staurogeniaeforme* (Schröd.) Chod. (*Staurogenia Schröderi* Schmidle) (fig. 47, G and H) has however been reported from various localities: cells 3–6 br. without spines. *T. heteracanthum* (Nordst.) Chod., in which the cells bear two curved spines of unequal length, and *T. apiculatum* (Lemm.) Schmidle, with a minute spine on one extremity of each cell, have each been recorded from only one locality.

Scenedesmus Meyen, 1829[2]. Coenobium of 4 or 8 (rarely 16) ellipsoid, oblong, or fusiform cells arranged with their long axes parallel and generally in one plane, either in a single or in two alternating rows. In some sp. the cells are longit. ridged and they are frequently furnished with variously disposed spines: commonly the terminal cells of the row differ in shape and other respects from the others. Chloropl. parietal, cup-shaped, with a lateral notch, often occupying the whole length of the cell, chlorophyll sometimes diffused throughout the protoplast, generally a single pyren. Multipl. by crosswise div. of the protoplast leading to formation of autocoenobia which are liberated by rupture or gelatinisation of the membrane of the parent-cell; syncoenobia are rare. Globular resting-spores are known in a few sp.

In the few sp. which have been carefully investigated each cell of the coenobium has been found to possess a delicate mucilage-envelope outside the cellulose wall; the large spines of *S. quadricauda* (Turp.) Bréb., for instance, as well as the connecting pads between the cells, are merely elaborations of this envelope[3].

Several investigators[4] have studied the growth of sp. of this genus under various cultural conditions and have shown that they may be made to assume very diverse forms, e.g. *Dactylococcus*-stages, *Chlorella*-like forms, etc. It is not clear, however,

[1] Chodat, Bull. Herb. Boissier, III, 1895, p. 114; Schröder, Ber. Deutsch. Bot. Ges. XV, 1897, p. 373.

[2] Brunnthaler, Hedwigia, LIII, 1913, p. 164; Chodat, 1913, p. 13; Smith, Arch. f. Protistenkunde, XXXII, 1914, p. 278; Smith, Trans. Wisconsin Ac. XVIII, 1916, p. 422; Wille, 1918, p. 1.

[3] cf. Senn, Bot. Zeit. LVII, 1899, p. 70.

[4] Chodat and Malinesco, Bull. Herb. Boissier, I, 1893, p. 184; Senn, loc. cit. p. 70; Grintzesco, Bull. Herb. Boissier, 2 sér. II, 1902, pp. 217, 406.

how far this polymorphism obtains in nature (see Smith, loc. cit., 1916, p. 424), although it is definitely established that *Dactylococcus infusionum* Naeg. (fig. 48, B) is a naturally occurring state of *Scenedesmus obliquus* (Turp.) Kütz. (cf. p. 101).

For most of the sp. a large number of varieties and forms have been described and specific delimitation is often a by no means easy matter. The most recent monograph of the genus is by G. M. Smith (1916), in which the bulk of the forms were studied under conditions of pure culture.

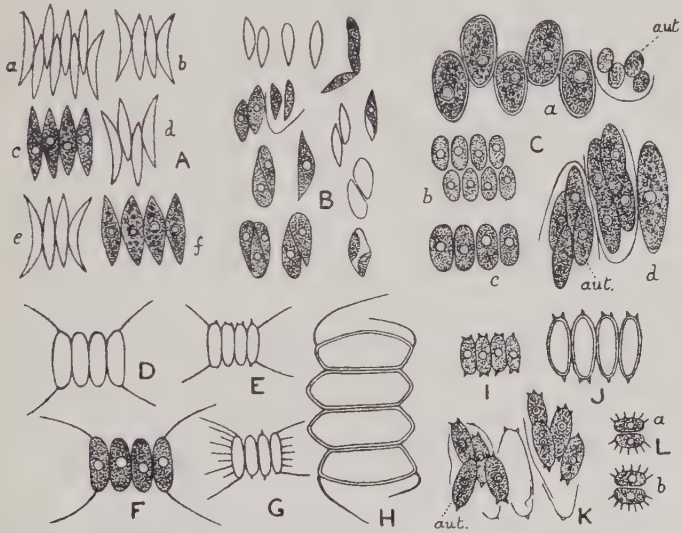

Fig. 48. A, *Scenedesmus obliquus* (Turp.) Kütz., from Bradford, W. Yorks. B, the state of *S. obliquus* known as *Dactylococcus infusionum* Naeg., from Bowness, Westmorland. C, *S. bijuga* (Turp.) Lagerh., from various localities. D–F, *S. quadricauda* (Turp.) Bréb., from Bradford, W. Yorks. G, *S. quadricauda* var. *horridus* Kirchn., from S. E. Surrey. H, *S. quadricauda* var. *maximus* W. & G. S. West, from Pilmoor, N. Yorks. I–K, *S. denticulatus* Lagerh. var. *linearis* Hansg.; I and J, from Westmorland; K, from Mayo, Ireland. L, *S. abundans* (Kirchn.) Chod. var. *spicatus* (W. & G. S. West) G. M. Smith (*S. spicatus* W. & G. S. West), from Saltburn, N. Yorks. (All ×520.) *aut*, autocoenobia.

There are some 12 Brit. sp., of which *S. quadricauda* (Turp.) Bréb. (fig. 48, D–F), *S. bijuga* (Turp.) Lagerh. (*S. obtusus* Meyen; *S. bijugatus* Kütz.) (fig. 48, C), and *S. obliquus* (Turp.) Kütz. (*S. acutus* Meyen) (fig. 48, A, B) are general and abundant. All three vary much in size (cells of large forms of *S. quadricauda* reaching a length of 30 μ and a breadth of 14 μ) and in other characters. They are regular constituents of the freshwater plankton, but occur most abundantly in stagnant water, especially in association with *Pediastrum Boryanum*,

Coelastrum sphaericum, etc. The cells of some of the sp. are furnished with tufts of gelatinous bristles, similar to those found in sp. of *Pediastrum*[1].

S. denticulatus Lagerh. var. *linearis* Hansg. (fig. 48, I–K) is widely distributed, but rarely occurs in such abundance as the three sp. above named. In *S. costatus* Schmidle and *S. acutiformis* Schröd. the cells possess prominent longitudinal ridges. *S. hystrix* Lagerh., whose cells bear numerous minute spines, and *S. granulatus* W. & G. S. West, where the walls bear three longitudinal rows of small warts, are very uncommon. Another remarkable sp., so far recorded from only one locality in the Midlands[2], is *S. Raciborskii* Woloszynska, where the four cells of the coenobium exhibit a radial disposition; syncoenobia are not uncommon in this sp., which approaches the genus *Tetradesmus* in the grouping of the cells.

Tetradesmus G. M. Smith, 1913[3] (*Victoriella* Woloszynska, 1914). Coenobia of four more or less ellipsoidal cells, often with a relatively thick wall, ranged parallel to one another in two planes. Chloropl. a single parietal plate, with a pyren. Reprod. by formation of autocoenobia within each cell, these being liberated by rupture of the membrane.

The only Brit. sp. is *T. cumbricus* G. S. West (cells 25–30 l.; 11–13·5 br.)(fig. 50, B–D), so far only recorded from the plankton of Ennerdale Water (West, 1915, p. 82).

Coelastrum Naegeli, 1849[4] (*Hariotina* Dangeard, 1889). Coenobium spherical or polyhedral, hollow, composed of 8, 16, or 32 (rarely 64) cells united to form a single peripheral layer, the whole surrounded by an obscure mucilage-envelope; cells globose or more or less polyhedral, often with a truncate projection (rarely two) on their free outer faces, joined either by the mucilage-layer on their contiguous faces or by more or less markedly projecting processes, in the latter case with spaces of variable size between the cells. Chloropl. parietal, bell-shaped, with a pyren. Reprod. by formation of autocoenobia, liberated by a split in the mother-cell wall or more rarely by its gelatinisation. Resting-spores have been observed in some sp.

Each cell of the coenobium is provided with a delicate mucilage-investment and the connecting pads and processes are develop-

[1] Petersen, Bot. Tidsskr. xxxi, 1912, p. 169.

[2] Griffiths, Journ. Linn. Soc., Bot. xliii, 1916, p. 430.

[3] G. M. Smith, Bull. Torrey Bot. Club, xl, 1913, p. 76; Chodat, 1922, p. 105.

[4] Naegeli, 1849, p. 97; Dangeard, Le Botaniste, i, 1889, p. 162; Chodat and Huber, Bull. Soc. Bot. France, xli, 1894, p. cxlii; Rayss, Mat. pour la Flore Crypt. Suisse, v, fasc. 2, 1915, p. 1; Wille, 1918, p. 23; Crow, Ann. of Bot. xxxviii, 1924, p. 398.

ments of this envelope[1]. As in the case of *Scenedesmus*, it has been shown for diverse sp. of *Coelastrum* that, under certain circumstances, the cells of the daughter-coenobia fall apart and both in structure and mode of multiplication then closely resemble those of *Chlorella*[2].

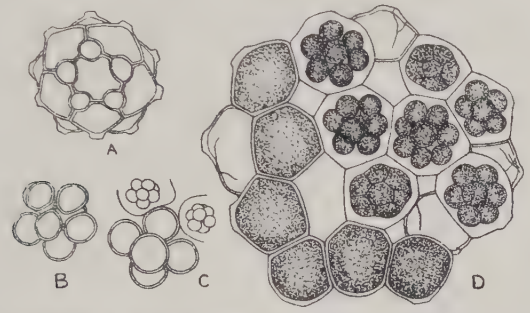

Fig. 49. A, *Coelastrum cambricum* Arch., from Lough Gartan, Donegal, Ireland. B–D, *C. sphaericum* Naeg.; B and C, small coenobia from near Penzance; D, large coenobium giving rise to autocoenobia, from Bowness, Westmorland. (All ×475.)

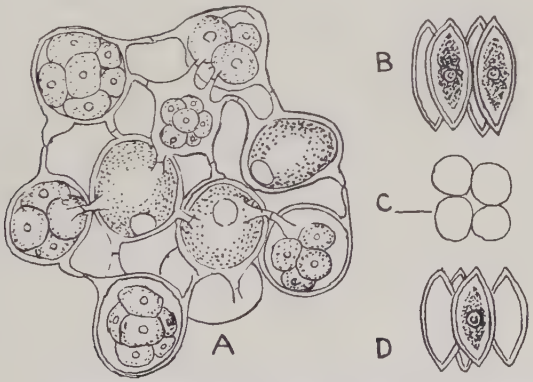

Fig. 50. A, *Coelastrum reticulatum* (Dang.) Senn, syncoenobium (after Chodat). B–D, *Tetradesmus cumbricus* G. S. West (after West, ×460), from Ennerdale Water, Cumberland; C, end-view.

The sp. of this well-defined genus occur at the margins of pools and lakes, although a number are essentially planktonic. There are seven Brit. sp., of which the two most frequent are *C. sphaericum* Naeg. (coenob. 18–92 br.; cells 4–23 br.) (fig. 49, B–D) and *C. cambricum* Arch. (*C. pulchrum* Schmidle) (fig. 49, A). In the former the cells are

[1] Senn, Bot. Zeit. LVII, 1899, p. 40.
[2] Senn, loc. cit. p. 47; Rayss, loc. cit. p. 41.

somewhat conical with a polygonal base, and in the latter they are more or less distinctly lobed and furnished with a truncate surface projection. Of far rarer occurrence are: *C. cubicum* Naeg. with hexagonal cells bearing three truncate processes and forming almost cubical coenobia; *C. microporum* Naeg. with almost spherical cells and very small intercellular spaces; *C. proboscideum* Bohlin with conical cells having an hexagonal base; and *S. schizodermaticum* F. Rich with a well-marked mucilage-envelope and little caps of cell-membrane split off from the outer surfaces of the cells[1].

C. reticulatum (Dang.) Senn (*Hariotina reticulata* Dang., *C. subpulchrum* Lagerh., *C. distans* Turn.), made the type of Dangeard's genus *Hariotina* (loc. cit.), differs from all other sp. of *Coelastrum* in the long narrow gelatinous, often curved and sometimes irregularly disposed processes by which the 4, 8 or 16 cells of the coenobium are connected. The young coenobia often remain for a relatively long period within the parent cell-membrane and, since the processes connecting the parent-cells persist, syncoenobia are of frequent occurrence; cells 6–24 br. (fig. 50, A).

GROUP 3. ULOTRICHALES

The faculty of limitless division of a purely vegetative type is the keynote to the group of the Ulotrichales, as to all other filamentous Algae. In such division the cell is partitioned by a septum which, in the majority of the Green Algae, develops as an annular ingrowth from the longitudinal walls and, subsequent to nuclear division, gradually cuts across the protoplast. The two cells thus produced adopt the membrane of the parent except for the intervening septum which is new and common to both. A consequence of this method of cell-increase is a tendency for the products to cohere and, as long as division takes place in one direction only, a filament is the necessary result. The origin of the filament may be regarded also from the mechanical point of view, the septa serving the purpose of giving mechanical stability to a developing cylindrical structure, such as might be obtained by the elongation in one direction of a *Chlorococcum*- or resting *Chlamydomonas*-cell. It is not without interest to carry this interpretation further and to note the effect of elongation and septation upon the almost spherical chloroplasts of such Algae. The cells of the resulting filaments would each contain an annular chloroplast having the shape of a hollow cylinder. Such a chloroplast is occasionally realised in *Ulothrix zonata* and in the genus *Pearsoniella*[2] recently described from South Africa. In other Ulotrichaceae the chloroplast

[1] F. Rich, New Phytol. xx, 1921, p. 234.

[2] Fritsch and Rich, Trans. Roy. Soc. South Africa, xi, 1924, p. 314.

represents a larger or smaller arc of a cylinder, in other words a curved parietal plate, with or without pyrenoids.

Vegetative division is, on the other hand, almost unknown among the unicellular and colonial Isokontae which have been considered in the preceding pages. The only outstanding exception is furnished by *Chlorosphaera* (p. 107), itself perhaps a reduced filamentous type. This is almost certainly true of *Pleurococcus* (*Protococcus*) which, in the present work, is regarded as a reduced member of the Chaetophorales (p. 209). The method of cell-increase (by rejuvenescence of the protoplast), typical of Volvocales and Chlorococcales, is however retained throughout

Fig. 51. A and B, *Ulothrix zonata* (Web. et Mohr) Kütz., from near Mells Abbey, E. Yorks (×500). C–F, *U. subtilis* Kütz., from near Mullion, Cornwall (×500): F shows development of a "palmella" condition. *a*, aplanospore; *za*, macrozoospore; *zi*, microzoospore.

the filamentous Algae in connection with asexual and sexual reproduction—in fact such a genus as *Ulothrix* is fundamentally distinguished from a *Chlamydomonas* or a *Chlorococcum* only by the vegetative division leading to the filamentous habit.

In *Ulothrix*, as in other Ulotrichaceae, there is no division of labour, except that the basal cell of young threads is developed as an attaching organ and is usually deficient in chlorophyll: otherwise all the cells are alike, each can grow and divide, produce zoospores, etc. (cf. fig. 51). Except in forms inhabiting flowing water, however, the filaments are only found attached in young stages; as they grow longer, they break across at one or more

points and thereafter are free-floating. Fragmentation of threads into short lengths remains as a common method of vegetative propagation throughout the period of active growth and attains its height in the terrestrial species of *Hormidium* (fig. 52, D) and *Stichococcus* (fig. 57); in the latter there is a great tendency for dissociation of the threads into the individual cells, so that even few-celled filaments are often rare.

The remaining reproductive methods have been most fully studied in *Ulothrix*[1]. In the production of swarmers, which usually commences near the apex and progresses towards the base of the filament, the protoplasts undergo successive division into two, four, eight, or more parts, the products being liberated through a small aperture formed on one side of the cell into a delicate evanescent mucilage-bladder (fig. 51, B); in the process of segmentation the superficial plasma-membrane and that bounding the central vacuole are not involved. It appears that three types of swarmers may be produced, viz. (*a*) quadriciliate macrozoospores formed in small numbers from the mother-cell and with an anterior stigma; (*b*) quadri- or biciliate microzoospores formed in larger numbers and with the stigma in the middle of the body (fig. 3, D); and (*c*) biciliate gametes which, though in general smaller, resemble the microzoospores. The macro- and microzoospores are positively phototactic to different light-intensities and can thus be separated; moreover the latter exhibit a much longer period of movement (2–6 days) than the former, which usually come to rest within 24 hours. The ciliation of the microzoospores seems to depend on their size, the larger being 4-, the smaller 2-ciliate. On germination they give rise to narrower filaments than those produced from macrozoospores, and this perhaps accounts for the diversity in size which is so often observed in collections of species of this genus. Pascher (loc. cit.) has shown that each of the three types of swarmers, though variable in size, varies about its own mean[2].

The gametes, which are usually liberated in the morning, are isogamous, though fusion only occurs between gametes from distinct parent-cells. The quadriciliate zygote soon rounds off to form a spherical thick-walled zygospore which, on germination, either forms zoospores or apparently more commonly aplanospores; in either case a number of new filaments are

[1] cf. especially Dodel, Jahrb. Wiss. Bot. x, 1876, p. 417; Klebs, 1896, p. 300; Pascher, Bibl. Bot. LXVII, 1907, p. 15.

[2] The movements of the microzoospores and gametes are frequently very strange, one cilium being kept more or less rigid and its extreme apex used as a pivot, while the other cilium exhibits violent movements causing a rapid lateral oscillation of the body.

produced. Parthenogenesis has been induced artificially by Klebs (1896, p. 321), the parthenospores behaving just like the normal zygospores.

Production of aplanospores (figs. 51, D; 53, F) is a frequent phenomenon, and the occasional *Palmella*-stages[1] are obviously but a modification, due to special conditions, of such aplanospore-formation. Species of *Ulothrix* also at times reproduce by akinetes (fig. 53, I) formed by thickening and partial gelatinisation of the walls and accumulation of food-reserves within the cells. It is interesting to note that the same striking diversity of reproductive methods is encountered also in *Stigeoclonium*, the central type of the Chaetophorales (p. 175).

The different genera of Ulotrichaceae are distinguished in the main on vegetative features, since in many cases little of their reproduction is known. *Hormidium* (fig. 52, D), however, apart from its characteristic chloroplast (p. 154) and prolific multiplication by fragmentation, is distinguished by its biciliate dorsiventral zoospores (fig. 52, F) which arise singly in the cells; sexual reproduction is only known in *H. flaccidum*, where the gametes, likewise produced one in each cell, are slightly anisogamous. The rare genus *Binuclearia* (fig. 54) is mainly distinguished from *Ulothrix* by the very marked thickening of the mature transverse walls, so that the protoplasts of recently divided cells appear in pairs separated by more or less wide mucilaginous tracts representing older septa. The akinetes, which are not uncommon, often germinate *in situ*, their thick walls which are ruptured on germination forming characteristic bands at intervals across the threads. In *Geminella* (fig. 55) and *Radiofilum* (fig. 56, D) the filaments are provided with a mucilage-envelope, which in the latter sometimes shows a fibrillar structure. Swarmers are not clearly established for any of these genera.

In all the Ulotrichaceae the cells contain a single parietal chloroplast, usually with one or more pyrenoids, and this is also true of the rare *Cylindrocapsa* (fig. 58), which is indeed often included in Ulotrichaceae in spite of its marked oogamy. The latter shows some striking analogies with that of *Oedogonium*, since the oogonia are considerably enlarged cells opening by a lateral pore to allow access of the spermatozoid to the single ovum, whilst the antheridia originate by active division of vegetative cells and each produce two brownish-red spermatozoids. Biciliate zoospores are also known, but the genus will well repay further study under natural conditions.

The Ulvaceae, mainly marine but with a few freshwater

[1] Cienkowski, 1876, p. 553.

representatives (fig. 59), appear to be a special development of the Ulotrichaceous type, resulting from a division of the cells in more than one direction (cf. *Schizomeris*, p. 153). Apart from the fact that the early stages in development are often filaments, scarcely distinguishable from an *Ulothrix*, the close relationship is shown by the cell-structure (single parietal plate-shaped chloroplast, with a pyrenoid) and the similarity in the reproductive processes.

In the very common freshwater genus *Microspora* (fig. 60) it is not improbable that we have merely another elaboration of the central type. According to G. S. West (1916 *a*, p. 289) there is a single parietal chloroplast taking the form of a very variable reticulum (fig. 60, E), parts of which are thickened to form somewhat bulging cushions apposed both to the lateral and terminal walls (fig. 52, G). Pyrenoids are absent, as in some species of Ulotrichaceae, but carbohydrates are stored as small starch-grains. In some of the species the cell-wall is composed of two overlapping portions, with the result that their filaments readily dissociate into H-shaped pieces (cf. fig. 60, C). In this respect they resemble those of the Heterokontan genus *Tribonema* (cf. p. 310), intermingled with which *Microspora* commonly occurs and with which it was long confused. In its reproductive methods *Microspora* shows many analogies with *Ulothrix*. Swarmers with four and two cilia (fig. 52, C) are recorded, as well as possible gametes; in addition aplanospores and akinetes are of common occurrence. There are thus scarcely grounds for placing the Microsporaceae in a group of their own, as has frequently been advocated[1].

The Prasiolaceae, represented by the very abundant terrestrial and aquatic genus *Prasiola* (fig. 61), stand somewhat apart from the forms hitherto discussed in the possession of an axile stellate chloroplast with a large central pyrenoid and the apparently complete absence of motile reproductive cells. A close relationship with the Eu-ulotrichales, previously considered, is improbable. Forms with axile and often more or less stellate chloroplasts are found in the Volvocales and Chlorococcales (e.g. *Asterococcus*, *Trebouxia*, *Dictyocystis*), and it is possible that they represent members of a distinct evolutionary series[2], of which *Prasiola* is the most elaborate form, but till there is adequate evidence the latter finds a more fitting place in the neighbourhood of the Ulvaceae with which its vegetative

[1] cf. Heering, 1914, p. 146.

[2] cf. also Lagerheim, Ber. Deutsch. Bot. Ges. x, 1892, p. 372. It should be noted however that parietal and axile chloroplasts occur side by side in other accepted series, e.g. Conjugatae.

differentiation has much in common. Here, however, the filamentous (*Hormidium*) stage (fig. 61, A, B) that always precedes the foliaceous one may last indefinitely, a condition that seemingly obtains especially in shady and dry situations.

Many will probably disagree with the inclusion of the Cladophoraceae in the group Ulotrichales, but the writer believes that this family finds at least as good a place there as among the Siphonales to which it has usually been referred. The Cladophoraceae are undoubtedly forms with a long history behind them, as shown by the coenocytic structure of their cells and

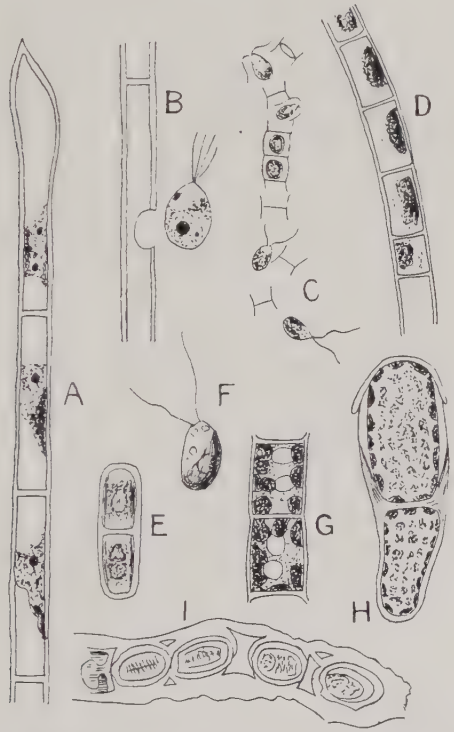

Fig. 52. A–B, *Uronema elongatum* Hodgetts (after Hodgetts, ×600), from King's Norton, Birmingham; B, liberation of macrozoospore. C and G, *Microspora tumidula* Hazen (after West); C, escape of zoospores (×375); G, showing chloroplast (×750). D–F, *Hormidium flaccidum* (Kütz.) A. Br. (after Klebs, ×750); E, young filament produced from a zoospore; F, zoospore. H, *Microspora amoena* (Kütz.) Lagerh. (after Meyer, ×550), young plant produced from an aplanospore. I, *Binuclearia tatrana* Wittr. (after Gutwinski, ×330), akinete-formation.

the frequent high morphological elaboration. Coenocytic types are not uncommon among Chlorococcales and it would not be surprising if the multinucleate condition had been retained in some of the filamentous forms originating from a Chlorococcaceous ancestry. In many of the genera of Cladophoraceae there is close resemblance in reproductive methods to Ulotrichaceae, saving that, owing to the large size of the cells, the swarmers are formed in very large numbers within them; there is however no development of special sporangia or gametangia, such as distinguishes the majority of the Siphonales. Although a number of the genera (*Cladophora* (fig. 64); *Pithophora* (fig. 65)) have richly branched filaments, this is not a universal characteristic, since in *Chaetomorpha* (fig. 62) there are no and in *Rhizoclonium* (fig. 63) few branches.

The special features of the cell-structure are easily related to the large size of the coenocytes. It would seem that in all cases the chloroplast is fundamentally single, consisting of a parietal reticulum with meshes of very varied size covering both the longitudinal and the transverse walls[1] and frequently extending into the cytoplasmic processes that traverse the cell-cavity; the pyrenoids are numerous and irregularly distributed. The number of nuclei varies from many in *Cladophora* down to one in some of the cells of *Rhizoclonium*[2] (only one in the marine *Spongomorpha*). A marked characteristic are the thick stratified membranes to which most Cladophoraceae owe their rough crisp feeling and probably their usual restriction to well aerated waters; the chief exception in this respect among the freshwater forms is constituted by *Pithophora*, whose real home is indeed in somewhat stagnant tropical waters[3].

Many Cladophoraceae are markedly perennial (especially *Cladophora*[4] and *Rhizoclonium*), unfavourable periods being tided over by a dormant condition in which the walls are even more prominently thickened, the cells sometimes irregularly swollen, and the contents laden with reserves; in *Cladophora* such dormant stages are often almost branchless. This is a state of wholesale akinete-formation without dissociation of the threads. *Pithophora*, however, develops specialised akinetes from a part only of each coenocyte (fig. 65), and this is the sole method of reproduction as yet known for this genus.

The larger Cladophoraceae are generally attached to some substratum and often frequent running water. The holdfasts

[1] Carter, Ann. of Bot. XXXIII, 1919, p. 469 et seq.
[2] Peterschilka, Arch. f. Protistenkunde, XLVII, 1924, p. 336.
[3] Fritsch, Ann. of Bot. XXI, 1907, p. 253.
[4] Fritsch and Rich, 1909, p. 40.

are relatively elaborate in conformity with the large size of the plants, and not uncommonly supplementary rhizoids are produced from the cells above the basal one. The peculiar short rhizoid-like branches of *Rhizoclonium* (fig. 63, B and C), which are not uncommonly practically absent, seem to have nothing to do with attachment and their function is dubious. In *Cladophora* and *Pithophora* there is apical growth of the branches, but in the other genera cell-division is not localised. *Cladophora* is also distinguished by the fact that zoospores and gametes are often only produced in the smaller branches of older plants whose main branch-system is thus essentially supporting in function; in *Pithophora* too production of akinetes is less frequent in the larger axes. In these respects the Cladophoraceae have gone beyond anything found in other Ulotrichales.

The position of the unique genus *Sphaeroplea* (fig. 66, B–E) is especially doubtful. With the Cladophoraceae, with which it is usually associated, it has nothing in common except the coenocytic construction and the undifferentiated "gametangia." In *S. africana* Fritsch[1], where the septa appear to develop incompletely and to be quite different from those of other Algae, a closer relationship with the Siphonales is possibly implied, but in that group also *Sphaeroplea* would occupy a very isolated position. For the present it may be allowed to stand as an exceptional member of the Ulotrichales, the annular chloroplasts[2], several of which occur in each coenocyte and give the threads a very handsome and striking appearance (fig. 66, C), constituting a possible indication of affinity. The outstanding features, apart from that just mentioned, are the absence of all attaching organs, the filaments being free-floating from the first, and the peculiar type of oogamy. Oogonia forming numerous (up to 100) ova and antheridia producing still more numerous spindle-shaped biciliate sperms are constituted by the ordinary coenocytes without change of form; a number of small pores formed in the walls admit of the escape of the spermatozoids on the one hand and of their penetration into the oogonia (fig. 66, E) on the other. The bright red oospores (fig. 66, B), which are known to survive a resting period of several years, on germination give rise to 2–8 biciliate zoospores. After the cessation of movement the new filament is initiated by a gradual elongation of each end. Production of zoospores by the ordinary threads has not yet been observed, but is manifestly probable.

In accordance with the foregoing remarks, four series can be distinguished among the Ulotrichales, viz.:

[1] Fritsch, 1918, p. 527.
[2] cf. footnote 2 on p. 173.

I. *Eu-ulotrichales*, in which the plant-body is a simple unbranched filament or a cellular expanse composed of uniform uninucleate cells without division of labour; chloropl. single, parietal, often with one or more pyrenoids; isogamous or oogamous.

II. *Prasiolales*, in which the plant-body is a simple unbranched filament, and later a cellular expanse, composed of uninucleate cells with an axile stellate chloropl.

III. *Cladophorales*, in which the plant-body is a simple or branched filament, sometimes with some division of labour among the cells which are uni- to multi-nucleate and have a single, more or less reticulate chloropl.; isogamous.

IV. *Sphaeropleales*, in which the plant-body is a simple unattached filament of coenocytes, each with a number of annular chloropl.: sexual reprod. oogamous, without differentiation of special sexual organs.

The following scheme will aid in the identification of the British genera:

Series I. *Eu-ulotrichales.*

A. Plant-body an unbranched filament, rarely showing longit. div. of the cells, chloropl. single and parietal, sex. reprod. where known not oogamous *Ulotrichaceae*

a. Filaments not readily fragmenting into the individual cells

1. Filaments without a prominent mucous envelope, cells cylindrical with truncate apices

* Filaments elongate, without a specially differentiated apical cell

† Cells evenly spaced, transv. walls not prominently thickened

§ Chloropl. annular or plate-shaped, usually extending round more than half the circumference of the cell and occupying its whole length, zoospores 4- or 2-ciliate, aquatic *Ulothrix*

§§ Chloropl. elliptical or circular in outline, often occupying only half the length of the cell, zoospores 2-ciliate, threads readily fragmenting, terrestrial or aquatic *Hormidium*

†† Cells in pairs, mature transv. walls very thick *Binuclearia*

** Filaments short, with an attenuated apical cell, epiphytic *Uronema*

2. Filaments with a prominent mucous envelope, cells cylindrical with hemispherical ends or subglobose or transversely extended

* Cells cylindrical, envelope structureless *Geminella*

** Cells subglobose or transversely extended, envelope sometimes striated at right angles to filament *Radiofilum*

b. Filaments readily fragmenting into the individual cells which are more or less cylindrical *Stichococcus*

B. Plant-body an unbranched filament, cell-walls thick and gelatinous, chloropl. single and parietal, sex. reprod. oogamous *Cylindrocapsaceae*

Only genus *Cylindrocapsa*

C. Plant-body a flat leaf-like expanse or a tubular thallus, chloropl. single and parietal, sex. reprod. isogamous *Ulvaceae*

a. Thallus when young vesicular, when adult a thin membranous expanse *Monostroma*

b. Thallus when adult an elongated tube *Enteromorpha*

D. Plant-body an unbranched filament, chloropl. of a number of parietal cushions joined to form an irregular network, without pyrenoids, cell-wall sometimes dissociating into H-shaped pieces *Microsporaceae*

Only genus *Microspora*

Series II. *Prasiolales.*

Only genus[1] *Prasiola*

Series III. *Cladophorales.*

Plant-body a branched (rarely unbranched) filament, composed of large usually thick-walled cells, membrane not mucilaginous, causing a rough and crisp feeling, sex. reprod. isogamous *Cladophoraceae*

a. Filaments without branches or with isolated rhizoid-like branches

1. Filaments broad, unbranched, usually with thick, lamellose walls *Chaetomorpha*
2. Filaments narrow, walls generally not very thick, with occasional short rhizoid-like branches *Rhizoclonium*

b. Filaments usually extensively branched

1. Plants large, often several inches from base to summit, chloropl. with numerous pyrenoids

* Membranes thick and stratified, branches usually originating from top of their supporting cell, akinetes not specially differentiated *Cladophora*

** Membranes thinner, branches originating a little below top of their supporting cell, special akinetes occupying only half the parent-cell *Pithophora*

2. Plants microscopic, chloropl. parietal, without pyrenoids *Chaetonella*

Series IV. *Sphaeropleales.*

Only family *Sphaeropleaceae*

Only genus *Sphaeroplea*

[1] cf. with *Bangia*, p. 421.

Series I. EU-ULOTRICHALES

Family 1. ULOTRICHACEAE

In this family the plant-body consists of simple unbranched filaments exhibiting no differentiation among the cells, except for the basal attaching cell often present in young stages; in a number of the genera the filaments are encased in mucilage-sheaths. The cells are uninucleate and contain a single parietal chloroplast, usually provided with pyrenoids. Reproduction is effected by fragmentation of the threads (commonly into unicellular portions in *Stichococcus*), by zoospores, aplanospores, and akinetes. Where sexual reproduction has been observed it is isogamous, the gametes being biciliate. The swarmers are formed, with or without division, from the contents of the ordinary cells.

Ulothrix Kützing, 1833[1] (*Hormiscia*[2] in the sense used by Rabenhorst (1868), Hansgirg, and De Toni). Filaments aquat., not attenuated at the apex, but frequently fixed by a unicell., simple or ramified basal "rhizoid"; cells commonly shorter than broad or as long as broad, sometimes swollen, in the larger sp. with thick lamellose walls. Chloropl. ring- or plate-shaped, usually extending round more than half the circumference of the cell and frequently occupying its whole length, with one or more pyrens. Reprod. by 4- and 2-ciliate zoosp. (p. 144), aplanosp., and akinetes formed by enlargement of certain cells frequently accompanied by gelatinisation of the outer portions of their walls. Sex. process isogamous; zygosp. smooth, spherical.

Seven sp. appear to be clearly recorded for this country, although their recognition in certain states may be a matter of difficulty. The best known is *U. zonata* (Web. et Mohr) Kütz. (fig. 51, A and B) which is widely distributed all over the Brit. Isles, occurring as bright green masses in streams, rivers, etc., more especially in the early spring; cells 15–70 br., with very thick and lamellose walls. An abundant

[1] Dodel, Jahrb. Wiss. Bot. x, 1876, p. 417; Klebs, 1896, p. 300; Hazen, 1902, p. 145; Haase, Archiv f. Hydrobiol. u. Planktonk. v, 1910, p. 167; Jörstad, Nyt Mag. f. Naturvidensk. LVI, 1919, p. 61.

[2] *Ulothrix* was established by Kützing (Flora, XVI, 1833, p. 517) for *U. zonata* two years before Fries' description of *Hormiscia* (Flora Scanica, 1835, p. 327). Areschoug's (Act. Roy. Soc. Sci. Upsala, sér. 3, VI, 1866, No. 2, p. 12) enlargement of *Hormiscia* was based on erroneous conceptions, as he included in it species having no affinity with each other. The original *Hormiscia* of Fries only included two Algae commonly placed in Areschoug's genus *Urospora*, which should perhaps be regarded as a synonym of *Hormiscia* Fries.

Brit. sp. is *U. subtilis* Kütz.[1] (fig. 51, C–F), with cells as long as broad (4–8). The var. *variabilis* (Kütz.) Kirchn. of this sp. is probably the most abundant member of the genus, being generally distributed in the stagnant waters of ponds, ditches, troughs, etc., as well as in cultivated soils (Bristol, 1920, p. 76); the threads may be 8–9 μ thick and the cells are one and a quarter to two and a quarter times longer

Fig. 53. A–F, *Ulothrix aequalis* Kütz.; A–D, from Putney Heath, Surrey; E and F, from Mitcham Common, Surrey. A, filament showing escape of microzoospores; B–D, germinating macrozoospores, C shows the same plants as B 48 hours afterwards, D is much further advanced; E, portion of filament forming akinetes; F shows two aplanospores which have taken 14 days to develop. G, *U. aequalis* Kütz. var. *cataeniformis* (Kütz.) Rabenh., from near Bradford, W. Yorks, showing escape of macrozoospores. H, *U. moniliformis* Kütz., from Wimbledon Common, Surrey; I, the same with akinetes. (All $\times 500$.) *a*, aplanospore; *ak*, akinete; *za*, macrozoospore; *zi*, microzoospore.

than their diameter. *U. aequalis* Kütz. (cells 12–22 br.) (fig. 53, A–F) and *U. moniliformis* Kütz. (cells 9–14 br.) (fig. 53, H–I) are other well-defined sp. A striking member of the genus, hitherto only recorded from Staffordshire (West, 1915, p. 81), is *U. spiroides* G. S. West, with very slender filaments (cells 1 br., four and a half to eight and a half times as long) forming a lax spiral.

Another Alga—*Schizomeris Leibleinii* Kütz.—which G. S. West

[1] It is possible that this species should be transferred to *Hormidium* (cf. Hazen, 1902, p. 162; Heering, 1914, p. 47) in view of the form of the chloroplast, but the zoospores seem to be of the *Ulothrix*-type; it is not improbable that two species are included under this name, one an *Ulothrix*, the other a *Hormidium*. The two authorities just cited regard the var. *variabilis* as a distinct species which is referred to *Ulothrix*.

(1904, p. 76) records as having been seen only from Stone Ghyll, Dodd Fell, N. Yorks, should perhaps be included here. He remarks: "I am doubtful as to the exact determination of the Yorkshire specimens, but they reminded one very much of a large *Ulothrix zonata*, attenuated both at the apex and base, the latter being fixed to rocks and stones in the spray of a waterfall. Longitudinal division of the cells had occurred at intervals, so that the filaments often consisted of a double row of cells." The writer has seen specimens from the Reddish Canal, Manchester, which differed from the published figures of *S. Leibleinii* in the irregular arrangement of the cells[1], but where uniseriate showed the same resemblance to *Ulothrix zonata* upon which West comments. Opinions differ as to the independence of *Schizomeris*[2], but if Hazen's (1902, p. 188) observations are confirmed, it would seem to be other than merely a state of *Ulothrix*.

Hormidium Kützing, 1849 pro parte; emend. Klebs, 1896[3] (*Ulothrix* sect. *Hormidium* Kützing, 1849; *Stichococcus* Gay, 1891 pro parte; *Hormococcus* Chodat, 1902 pro parte). Filaments terrestr. or aquat., not attenuated at the apex, usually without a specially differentiated attaching cell; cells cylindrical with truncate apices, commonly as long as or longer than broad, with thin walls. Chloropl. usually elliptical or circular in outline, generally occupying about half the length of the cell, mostly with one pyren.; in the colourless plasma at either end of the cell there are commonly prominent vacuoles containing granules of uncertain nature. Reprod. abundantly by fragmentation (esp. in the terrestr. sp.), by biciliate often (always?) somewhat dorsiventral zoosp. (formed singly in the cells), aplanospores, and (in one sp.) slightly anisogamous gametes: akinetes also known.

The exact limits of this genus are extremely doubtful and there is still much confusion with *Ulothrix* and *Stichococcus* (q.v.). It is probable that various investigators have dealt with quite different Algae, even in the case of the common *H. flaccidum* (Kütz.) A. Br. (*Ulothrix flaccida* Kütz.) to which the above generic description more particularly applies. The abundant terrestr. form of this sp. is distinguished by its chloropl. and its peculiar zoospores which the writer has seen in cultures of Dr N. Carter's and found to accord with the description of Klebs (loc. cit.). This Alga (fig. 52, D–F) is found especially on damp heavy soils: the cells are 6–14 br. and of very varying length, though commonly longer than broad; at times of drought they are often laden with small fat-bodies. Whether the

[1] cf. also Fritsch and Rich, Trans. Roy. Soc. S. Africa, xi, 1924, p. 317.

[2] See for instance Cienkowski, 1876, p. 558; Heering, 1914, p. 37.

[3] Klebs, 1896, p. 326; Klerker, Flora, lxxxii, 1896, p. 90; Wille, Svensk Bot. Tidskr. vi, 1912, p. 447; Brand, Ber. Deutsch. Bot. Ges. xxxi, 1913, p. 66; Chodat, 1913, p. 138; Piercy, Ann. of Bot. xxxi, 1917, p. 513.

somewhat similar aquat. form really belongs to this sp. is doubtful. *H. nitens* Menegh. emend. Klebs, another terrestr. sp. recorded by Bristol from cultivated soils, is hardly distinguishable from *H. flaccidum* except by the manner of its growth in cultures (cf. also Hazen, 1902, p. 165). *H. rivulare* Kütz., a form inhabiting flowing water, may or may not belong to the same genus; the threads show knee-shaped bends and frequent formation of rhizoid-like branches; cells 4–11 br. Another rather doubtful sp. is *H. dissectum* Chod. (*Stichococcus dissectus* Gay) (fig. 57, C), in which fragmentation of the threads is very marked. West (1904, p. 80) regarded it as a possible form of *H. flaccidum*.

Binuclearia Wittrock, 1886[1]. Filaments aquat., attached when young by a tubular outgrowth from the basal cell, sometimes with an ill-defined mucous envelope; cells cylindrical with firm walls, older transv. septa strongly thickened and lamellose, so that recently divided cells appear arranged in pairs. Chloropl. parietal, occupying the middle of the cell, without a distinct pyren.; at either end of the protoplast a prominent granule of varying size is sometimes to be encountered. Reprod. by akinetes, which often germinate without separating from one another, their thick ruptured walls forming bands across the threads at intervals (fig. 52, I); zoosp., which are imperfectly known, and aplanosp. also recorded.

Fig. 54. A–E, *Binuclearia tatrana* Wittr., from Lewis, Outer Hebrides (×440).

B. tatrana Wittr. (figs. 52, I; 54), the only sp., is not uncommon at the margins of subalpine tarns and lakes, especially if boggy; cells 6–9 br. A detailed investigation of its life-history is very much to be desired. A resemblance to Heterokontae has frequently been pointed out, but the chloropl. is against any real affinity. Fat-like substances appear to accumulate during assimilation; the presence of starch is doubtful.

Uronema Lagerheim, 1887[2]. Filaments aquat., relatively short, consisting of cylindrical cells with thin walls, the apical

[1] Wittrock, Bot. Notiser, 1886, p. 134; Wittrock, Bih. K. Sv. Vet.-Akad. Handl. XII, 1887, Afd. III, No. 1; Schröder, Forschungsber. Biol. Stat. Plön, VI, 1898, p. 19.

[2] Lagerheim, Malpighia, I, 1887, p. 517; West and West, 1903, p. 37; Hodgetts, New Phytol. XVII, 1918, p. 159.

cell acuminate, the basal one elongate and secreting an attaching disc. Chloropl. parietal, sometimes lobed, occupying the middle of the cell, with 1–3 pyrens. Reprod. by 4-ciliate zoosp. of which 1–2 are produced in each cell; globular aplanosp. also recorded.

Two sp. are known in Brit., but both are rare. *U. confervicolum* Lagerh. (cells 4–6 br.; 2–3 times as long) is recorded from the Orkneys and Shetlands, as well as from Esher Common, Surrey. *U. elongatum* Hodgetts, with much longer cells (4·4–9·6 br.: 4–13 times as long) (fig. 52, A–B), is known from the Midlands.

Further observations are necessary to settle whether these sp. are really independent forms or merely stages of *Ulothrix* or other filamentous Isokontae[1]. It may be that they belong to a highly reduced member of the Chaetophorales.

Geminella Turpin, 1828; emend. Lagerheim, 1883[2] (incl. *Hormospora* de Brébisson, 1840; *Gloeotila* Kützing, 1843; *Planctonema* Schmidle, 1903). Filaments aquat., usually free-floating, provided with a more or less prominent cylindrical mucous envelope which is hyaline and homogeneous; cells oblong, oblong-cylindrical, or elliptical, with broadly rounded extremities, rarely grouped in pairs. Chloropl. parietal, disposed as an equatorial band, with or without a pyren.; cell-wall thin and delicate. Soon after division the transv. septa split, while the ends of the cells round off and often become separated by mucilage. Reprod. very incompletely known, by fragmentation, akinetes, and 2-ciliate zoosp.

Of the six Brit. sp. the most frequent is *G. mutabilis* (Bréb.) Wille (*Hormospora mutabilis* Bréb.) (fig. 55, A) which occurs principally in bogs, especially amongst *Sphagnum*, in which localities sp. of *Ulothrix* do not usually exist; cells 16–19 br., $1\frac{1}{2}$–$1\frac{3}{4}$ times longer than broad, generally in contact. *G. ordinata* (W. & G. S. West) Heering (*Hormospora ordinata* W. & G. S. West) (fig. 55, B) is smaller (cells 5·8 br.) and much rarer; here the cells are usually separated. *G. interrupta* Turp. (fig. 56, A–C), which frequently shows arrangement of the cells in pairs, is found rarely in stagnant pools; cells 6·5–7 br. In *G. protogenita* (Kütz.) (*Gloeotila protogenita* Kütz.) (fig. 55, C–E) the small cells (3–4·5 br.) are not so completely separated and pyrens. are lacking; it is a very rare sp. found in bogs and boggy pools and is also stated to occur on damp soil.

The writer is altogether in agreement with G. S. West (1916 *a*, p. 287) as to the inclusion of *Hormospora* and *Gloeotila* in *Geminella*. A well-defined genus is thus obtained, about whose life-history however very little is known. Heering (1914, p. 48) keeps *Gloeotila*

[1] cf. Gaidukov, Ber. Deutsch. Bot. Ges. XXI, 1903, p. 522; Hodgetts, loc. cit. p. 165.

[2] Lagerheim, Öfvers. K. Sv. Vet.-Ak. Förhandl. XL, 1883, No. 2, p. 68; Borzi, Studi Algologici, II, 1895, p. 357.

distinct, whilst Wille (1909, p. 71) refers it to *Stichococcus*, but the occurrence of zoosp. (Borzi, loc. cit.) speaks against this. Cienkowski[1] and others have regarded the sp. of *Geminella* as stages in the life-cycle of *Ulothrix*; to prove this it would be necessary to show that sp. of the former, removed from their natural habitats, could be caused to give rise to sp. of the other genus.

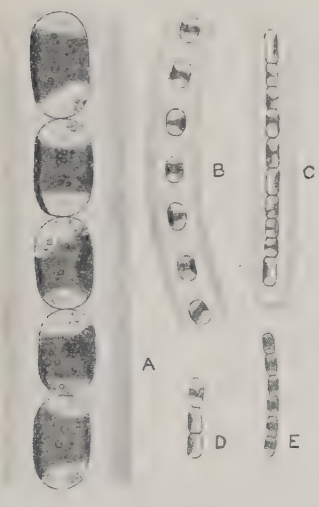

Fig. 55. A, *Geminella mutabilis* (Bréb.) Wille, from near Mullion, Cornwall. B, *G. ordinata* (W. & G. S. West) Heering, from Cam Fell, W. Yorks. C–E, *G. protogenita* (Kütz.), G. S. West, from Pilmoor, N. Yorks (×440).

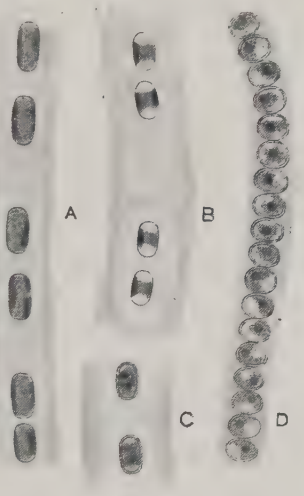

Fig. 56. A–C, *Geminella interrupta* Turp.; A and B, from near the Lizard, Cornwall (×440); C, two akinetes, from Glen Tummel, Perthshire (× 350). D, *Radiofilum flavescens* G. S. West, from Wicken Fen, Cambridgeshire (×440).

Radiofilum Schmidle, 1894[2]. Filaments aquat., free-floating, short and fragile or long and flexuous, enclosed in a cylindrical mucilage-sheath exhibiting a more or less distinct fibrillar structure; cells globose, ellipsoid, or sublenticular, free and distant or joined by a narrow mucilaginous bridge, always forming moniliform threads. Chloropl. with 1–2 pyrens.; cell-wall thick, composed of two equal halves, one of which is reconstituted in cell-division. Reprod. doubtful (zoosp.?).

[1] Cienkowski, 1876, p. 554.

[2] Schmidle, Flora, LXXVIII, 1894, p. 47; G. S. West, Journ. of Bot., 1899, p. 57; Brunnthaler, Österr. Bot. Zeitschr. LXIII, 1913, p. 1. The last-named suggests that *Radiofilum* is a filamentous Desmid, a view for which there is no adequate evidence (cf. also West, 1916 *a*, p. 287).

Two sp. have been recorded in this country, but both are rare. The type sp., *R. conjunctivum* Schmidle (incl. *R. apiculatum* W. & G. S. West), which has short fragile filaments of broadly ellipsoid cells (6 br.) with a wall distinctly composed of two pieces, is known only from Berkshire (Griffiths, 1922, p. 10). *R. flavescens* G. S. West (fig. 56, D) is larger (cells 7·5–10·5 br.), with much longer flexuose filaments and broad elliptical cells with yellowish-green chloropl.

Chodat and Topali[1] have recently described an apparently closely allied form under the name of *Interfilum paradoxum*, in which the chains of cells are occasionally branched.

Stichococcus Naegeli, 1849[2] (*Hormococcus* Chodat, 1902 pro parte). Filaments terrestr., very short, readily fragmenting, often into the individual cells; cells cylindrical with rounded ends and thin walls. Chloropl. frequently not occupying more than half the cell-wall, devoid of a pyren. Reprod. as far as known solely by fragmentation.

Much confusion exists with reference to the terrestrial members of Ulotrichaceae. Apart from the sp. of *Ulothrix* found in the subterranean soil-community (Bristol, 1920, p. 76), there appear to be two well-marked sets of forms; in one the filamentous tendency is strong, the chloropl. are well-defined and have pyrens., and reprod. by zoosp. is known (*Hormidium*, p. 154); in the other the filamentous tendency is weak, the chloropl. are not so well-defined and devoid of pyrens., and fragmentation is the only method of reprod. known (*Stichococcus*) (cf. however Hazen, 1902, p. 159).

Fig. 57. A, *Stichococcus bacillaris* Naeg., from Saltaire, W. Yorks. B, form of *Hormidium flaccidum* (Kütz.) A. Br. (?), from Barnes Common, Surrey[3]. C, *H. dissectum* Chod., from damp walls, London. D, *Stichococcus variabilis* W. & G. S. West, from Bradford, W. Yorks (× 440).

Stichococcus bacillaris Naeg. (fig. 57, A) is abundant on damp earth, walls, palings, etc.; cells 2·7–3·8 br. *S. variabilis* W. & G. S. West (fig. 57, D) forms a thin green stratum on wet stones in the neighbour-

[1] Chodat, 1922, p. 66.

[2] Naegeli, 1849, p. 76; Gay, 1891, p. 77; Brand, Ber. Deutsch. Bot. Ges. xxxi, 1913, p. 64; Chodat, 1913, p. 144.

[3] This figure shows what West (1904, p. 79) calls fragmentation of the chloroplast, but it may be doubted whether t really belongs to any of the Algae here considered.

hood of waterfalls; the cells (3–6 br.) are very irregular in form and the chloropl. often devoid of a pyren., though sometimes with two according to West. *S. scopulinus* Hazen, recorded from wet stones in Warwickshire (West, 1911, p. 84), is probably a sp. of *Hormidium*[1].

Family 2. CYLINDROCAPSACEAE

This family comprises solely the genus *Cylindrocapsa* Reinsch, 1867[2]. Filaments unbranched, aquat.,

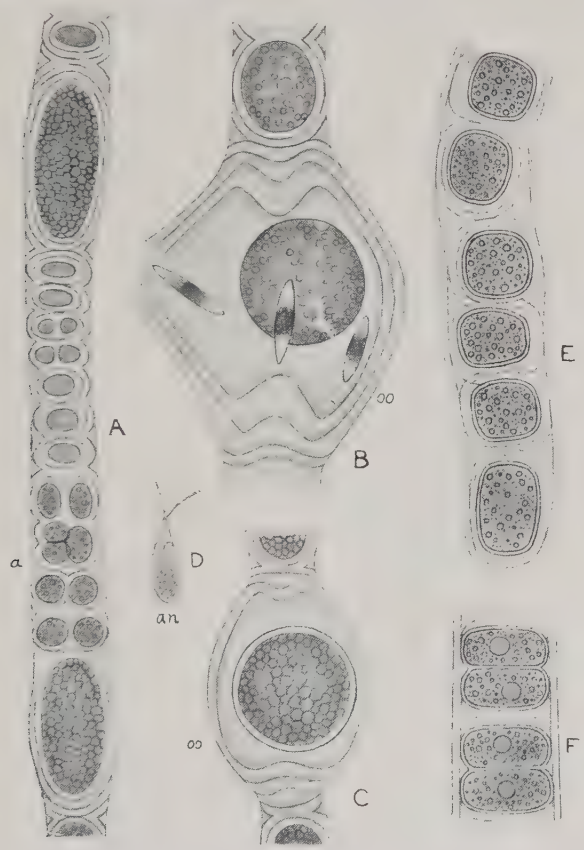

Fig. 58. A–D, *Cylindrocapsa involuta* Reinsch (after Cienkowski, ×480). *a*, antheridium; *an*, spermatozoid; *oo*, oogonium. B shows the oogonium at the time of fertilisation, C an oogonium with a ripe oospore. E and F, *C. conferta* West, from Bowness, Westmorland (×520).

[1] cf. Chodat, 1913, p. 145. Heering (1914, p. 48) refers it to *Gloeotila*, with which there does not appear to be much resemblance.

[2] Cienkowski, 1876, p. 560; W. West, Journ. Roy. Microscop. Soc., 1892, p. 735.

often enclosed within a thick close-fitting lamellose sheath; cells of young filaments disposed in a single series, but in older threads, as a result of longit. and oblique div., irregularly arranged, each with a stratified gelatinous wall; cells subrectangular, ellipsoid, or subtriangular in shape and sometimes placed in pairs at intervals along the filament. Chloropl. parietal, massive and often ill-defined, with a single pyren. Reprod. by (*a*) detachment of single cells or groups of cells which grow out to form new threads; (*b*) spherical or ovoid 2-ciliate zoosp. (with a red pigment-spot and two contr. vacs.), one, two, or four of which are formed from a cell; and (*c*) an oogamous sex. process. Antheridia produced by active div. of certain cells and arranged in one, two, or four longit. series within the sheath (fig. 58, A, *a*); each antheridium gives rise to two sperms of a form similar to that of the zoosp., but brownish-red in colour and with two short cilia (fig. 58, D). Oogonia originating by enlargement of the vegetative cells and forming swollen spherical or ovoid structures, with a thick stratified wall opening by a lateral pore (fig. 58, B and C); ovum single and spherical. Oospore not filling the oogonium, with a thick wall and brick-red contents (fig. 58, C).

Three sp. are recorded for the Brit. Isles, but all are rare. *C. involuta* Reinsch (fig. 58, A–D), the only sp. of which the sex. reprod. has been worked out, is known from Ireland; cells spherical or elliptical, 23–30 br. *C. conferta* West (fig. 58, E–F), with subrectangular or flattened cells (21–26 br.), is recorded from the English Lake District, whilst *C. geminella* Wolle var. *minor* Hansg., with narrower and longer cells (12–15 br.), has been found in various parts of the Midlands.

Family 3. ULVACEAE

This is essentially a marine family, with a few freshwater representatives, distinguished by the production of a parenchymatous thallus as a result of the division of the cells in more than one direction. The plant-body consists of flat ribbons or plates or more rarely it is vesicular or intestiniform. The cells are arranged to form one (*Enteromorpha*, *Monostroma*) or two layers (*Ulva*), are generally closely aggregated, and placed with their long axes at right angles to the surface (fig. 59, D). They are uninucleate and contain a single parietal chloroplast, often with deeply incised or lobed margins and including a single pyrenoid. Reproduction is known to take place (*a*) by budding off of small parts of the thallus, (*b*) by zoospores, which in *Ulva* are 4- and in *Monostroma* 2–4-ciliate, and (*c*) by the conjugation of isogamous biciliate gametes, eight (4–16) of which are usually produced from a cell (fig. 59, E–J). The resulting 4-ciliate zygote

soon loses its cilia and gives rise to a spherical zygospore, which sometimes germinates immediately.

In *Ulva* and *Enteromorpha* both zoospores and zygospores give rise to a short thread, the cells of which soon exhibit longitudinal division, so that a flat expanse results which gradually becomes 2-layered. The hollow thalli of *Enteromorpha*

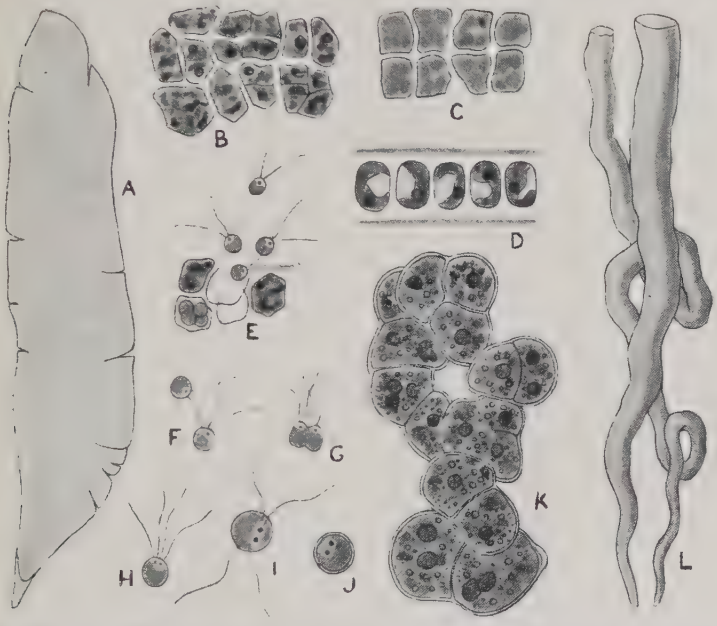

Fig. 59. A–K, *Monostroma membranaceum* W. & G. S. West, from Mitcham Common, Surrey. A, nat. size; B and C, portions of thallus; D, section of thallus; E, cells with escaping gametes (× 566). F–J, fusion of gametes (F–H, × 566; I and J, × 790). K, young plant developed from zygospore (× 566). L, *Enteromorpha intestinalis* (L.) Link, from Frizinghall, W. Yorks (nat. size).

(fig. 59, L) are produced by subsequent separation of the two layers. In *Monostroma* there appears often to be no filamentous stage, the zygospore, according to Reinke[1], dividing into eight peripherally arranged cells enclosing a central cavity; by gradual enlargement a vesicular thallus is produced which mostly opens out later to form a flat expanse. Chodat[2] gives a rather different account for *M. bullosum* (Roth) Wittr. The young

[1] Reinke, Jahrb. Wiss. Bot. XI, 1878, p. 533.

[2] Chodat, Bull. Soc. Bot. de France, XLI, 1894, p. CXXXIV; Chodat, 1902, p. 255.

thalli are usually attached to some substratum by rhizoids, which in older plants often form compact attaching discs.

Monostroma Thuret, 1854[1]. Thallus in the adult plant always a thin membranous plate, but in the young state it may be vesicular and attached to water-plants, opening out as it grows and gradually becoming free-floating; cells rounded or more or less angular, often in groups of four, in a single layer. Reprod. by budding off of small flat portions from the surface of the thallus, by zoosp. with two or four cilia, and by 2-ciliate gametes.

Only two sp. of this genus inhabit freshwaters in Gt Britain and neither is at all common. *M. bullosum* (Roth) Wittr. has rounded cells (6–12 br.), arranged in T-shaped groups of fours and with their greatest length parallel to the surface of the thallus, whilst in *M. membranaceum* W. & G. S. West (fig. 59, A–K) the cells (8–20 br.) are much more compact, angular, and elongated at right angles to the surface.

Enteromorpha Link, 1820[2]. Thallus elongated, not expanded, usually tubular and intestiniform, sometimes reaching a considerable length and often branched, green, yellowish-green, or pale olive-green in colour; cells rounded or polygonal, in a single layer. Reprod. imperfectly known, but 4-ciliate zoosp. and 2-ciliate gametes have been recorded in a few cases.

The only common Brit. freshw. sp. is *E. intestinalis* (L.) Link (fig. 59, L), an Alga which also occurs in brackish water and in the sea. It is widely distributed in the large drains and dykes in the East of England, and also occurs frequently in canals, rivers, and ponds in other parts of the country. *E. percursa* (Ag.) J. Ag., recorded from brackish water in the Midlands (Grove, 1920, p. 33), is a sp. in which the thallus forms a compact filament composed of 1–4 rows of cells.

Sp. of *Enteromorpha* and *Ulva* are often abundant in estuaries, where there is some pollution from sewage.

Family 4. MICROSPORACEAE

The only genus is

Microspora Thuret, 1850; emend. Lagerheim, 1888[3]. Filaments unbranched, probably often free-floating from the first, composed of cylindrical or slightly swollen cells with cellulose walls which are sometimes thin, but more usually somewhat thickened and stratified; in some (but by no means in all) sp. the walls are evidently composed of two overlapping halves (fig. 60, F), so

[1] Wittrock, Försök till en Monogr. öfver algslägtet *Monostroma*, Upsala, 1866; Reinke, loc. cit.; Chodat, loc. cit.; West and West, 1903, p. 36.

[2] Areschoug, Bot. Notiser, 1876, p. 129.

[3] Lagerheim, Flora, LXXII, 1889, p. 182; Hazen, 1902, p. 167; Meyer, Ber. Deutsch. Bot. Ges. XXXI, 1913, p. 441; West, 1916 *a*, p. 288.

that the threads dissociate into pieces which appear H-shaped in optical section (figs. 52, C; 60, C), each piece consisting of a septum and portions of the lateral walls of the two adjacent cells. Cells with a single, often large central nucleus and a reticulate chloropl. (fig. 60, E) spread over the whole inner surface of the wall and thickened at certain points to form parietal cushions (fig. 52, G): pyrens. are absent, but there are often small starch-grains. Reprod. by (*a*) ovoid or subellipsoid 2-ciliate zoosp. (4-ciliate zoosp. also recorded), with two contr.

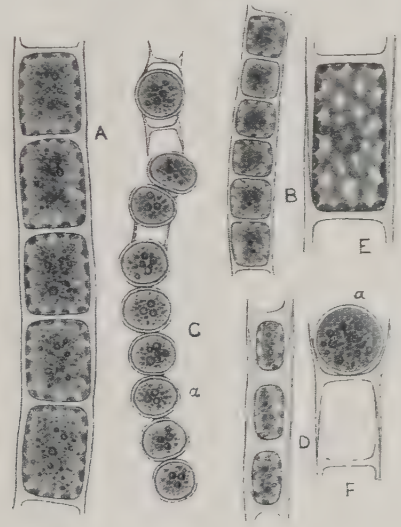

Fig. 60. A, *Microspora amoena* (Kütz.) Lagerh., from near Senens, Cornwall. B and C, ? *M. abbreviata* (Rabenh.) Lagerh.; B from Tremethick Moor and C from St Just, Cornwall. D, *M. pachyderma* (Wille) Lagerh., from near Land's End, Cornwall. E and F, forms of *M. amoena* (Kütz.) Lagerh.; E, from Shipley, W. Yorks, to show the chloroplast; F, from New Forest, Hants. *a*, aplanospores. (All ×520.) E is *M. amoena* var. *crassior* Hansg.

vacs. at the anterior end, formed singly or more rarely to the number of 2, 3, 4, 8, or 16 per cell (fig. 52, C); (*b*) spherical aplanosp. which develop a thin or thick wall and are usually produced singly (fig. 60, C); and (*c*) thick-walled square or rectangular akinetes, generally formed in long chains. Sex. reprod. not certainly established.

In the germination of the zoosp. or aplanosp. the first div. is of the normal type, the smaller of the two resulting cells playing no further part in the development of the thread and probably corresponding to an attaching cell, even when not functional.

In those sp. (e.g. *M. amoena* (fig. 52, H)) which possess an H-shaped structure, this is developed already at the second div. by transv. rupture of the wall and intercalation of a cylindrical strip of membrane from the middle of which a septum gradually grows across the cell-cavity. In other cases (e.g. *M. stagnorum*) normal transv. div. appears to occur throughout the life of the filament (cf. West, 1916 *a*, fig. 185, H–J).

Sp. of this genus are widely distributed in the Brit. Isles, usually favouring stagnant pools; they are cold water forms found especially in the winter months. Of the six that have been recorded, *M. floccosa* (Vauch.) Thur. (cells 14–18 br.) and *M. amoena* (Kütz.) Lagerh. (cells 20–25 br.) (fig. 60, A, E, and F) are the most abundant and often occur in small ponds and horse-troughs; in the latter the H-shaped structure is usually very clear, less so in the former. In *M. stagnorum* (Kütz.) Lagerh. (cells 5-9·5 br.) the filaments always break at the transv. walls and the chloropl. does not generally occupy the whole cell. Rarer sp. are *M. abbreviata* (Rabenh.) Lagerh. (cells 5–11 br.) (? fig. 60, B and C) and *M. pachyderma* (Wille) Lagerh. (cells 9–12 br.) (fig. 60, D), the latter with specially thick walls. *M. amoena* has been commonly recorded in the plankton (West and West, 1905, p. 497).

Series II. PRASIOLALES

Family PRASIOLACEAE

The only genus is

Prasiola Agardh, 1821[1] (incl. *Schizogonium* Kützing, 1843[2]; *Hormidium* Kützing, 1843 pro parte). Thallus commonly terrestr., either simple filaments[3] composed of flat cells or irregular leafy expansions consisting of one (rarely two) layers of quadrate or polygonal cells, with their long axes at right angles to the surface and more or less distinctly arranged in groups of four; attaching rhizoids may or may not be produced from the cells at the edge of the thallus. Cell-walls strong, rigid, and hyaline, thick and confluent in the expanded thalli; chloropl. axile, stellate, with one pyren.; obvious vacuoles usually lacking; one nucleus. Motile reprod. elements unknown. Reprod. takes place in the filamentous (so-called *Hormidium*-) stage by fragmentation, usually brought about by the dying off of isolated cells, which

[1] Imhäuser, Flora, LXXII, 1889, p. 233; Gay, 1891, p. 80; Lagerheim, Ber. Deutsch. Bot. Ges. X, 1892, p. 366; Wille, Vidensk. Selsk. Skrift., Christiania, 1900, No. 6, p. 13; Brand, Hedwigia, LIV, 1914, p. 295.

[2] All authorities now appear to be agreed in placing this as a synonym of *Prasiola*.

[3] Brand (loc. cit. p. 303) and Hodgetts (New Phytol. XIX, 1920, p. 260) have recorded branching of the filaments.

appear at first as deep green biconcave cells with homogeneous contents; in the leafy thalli budding often occurs from the margins, leading to the detachment of single cells, short threads, or small expanses. Thick-walled akinetes are also formed, which can grow directly into new plants or on germination give rise to a number of aplanosp. from which the new plants are produced. The *Hormidium*-stage represents the juvenile condition from which the leafy expanses are sooner or later formed; under certain conditions (e.g. shade), however, the filamentous stage may persist indefinitely.

In a variety of *P. mexicana* J. Ag., Lagerheim (loc. cit.) described a formation of "tetraspores" produced by a vertical

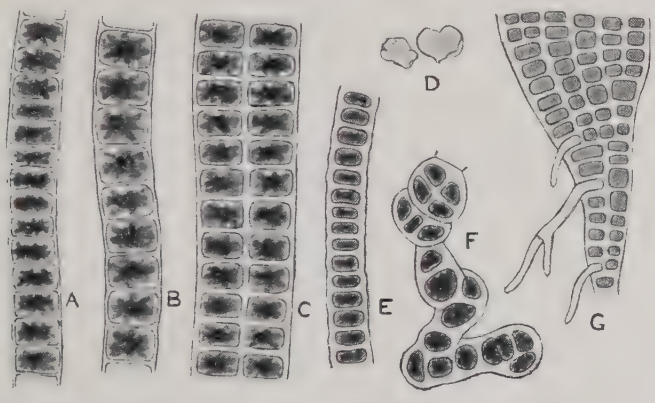

Fig. 61. A–C, *Prasiola crispa* forma *muralis* from Bradford, W. Yorks (×500). D–G, *P. crispa* (Lightf.) Menegh.; D, from Bradford, W. Yorks (nat. size); E, simple filament, from Helvellyn, Cumberland; F, portion of irregular filament from Wimbledon Common, Surrey (×500); G, basal portion of broader thallus, from Bradford, W. Yorks (×400).

and a horizontal division in somewhat enlarged and rounded cells; the further fate of these spores was not observed and a similar method of reprod. has not so far been recorded in other sp. Lagerheim's observation, together with the considerable similarity in vegetative construction, has led some to believe in an affinity between Prasiolaceae and Bangiales (cf. p. 421); there are however considerable differences.

Sp. of this genus occur on moist earth, rocks, stones, old walls, trunks of trees, etc. A very wide-spread Alga is *P. crispa* (Lightf.) Menegh. (which includes *Hormidium murale* Kütz.; *Schizogonium crispum* (L.) Gay; and *Ulothrix radicans* Kütz.) (fig. 61, D–G); its forma *muralis* (Kütz.) G. S. West (incl. *Prasiola parietina* (Vauch.) Wille; *Schizogonium murale* Kütz.; *Hormidium parietinum* Kütz.)

(fig. 61, A–C) is likewise abundant: in the former the cells are 7–14 br. and in the latter 9–18 br. These two forms are found all over the Brit. Isles, having a decided preference for the neighbourhood of towns, where they are found frequently under walls and as a green carpet between the paving stones of quiet streets. They require little moisture and can withstand considerable desiccation[1]. Associated with them are usually numerous *Rotifer vulgaris* and testaceous Rhizopods, such as *Trinema acinus*. Letts[2] has shown that specimens of *P. crispa* growing on contact beds may contain as much as 8·94 per cent. of nitrogen in the dried material. This accords with the abundant occurrence of sp. of *Prasiola* at points where there is a plentiful supply of nitrogenous food, e.g. the Penguin rookeries of the Antarctic[3].

Series III. CLADOPHORALES

Family CLADOPHORACEAE

The members of this family are widely distributed aquatic forms in which the filaments are commonly richly branched (exceptions: *Chaetomorpha*, *Rhizoclonium*) and composed of large, often elongate cells, mostly containing a considerable number of small nuclei which are stated to be embedded in the chloroplast. The latter is a somewhat diffuse parietal film, usually more or less perforated or reticulated and often with irregular strands projecting into the cell-cavity[4]; there are numerous scattered pyrenoids. According to earlier accounts the chloroplast sometimes breaks up in the older cells into a number of pieces, some with and some without pyrenoids, but it is uncertain whether this is correct. Very little, if any, mucilage is secreted by these Algae and they always have a rough and crisp feeling, while the absence of a mucous coat causes them to be frequently loaded with epiphytes (e.g. the Diatoms *Gomphonema* and *Cocconeis*). The growth of the thallus is effected by elongation and transverse division of the apical cells in *Cladophora* and *Pithophora*, but is intercalary in the other genera. A basal attaching cell is generally well developed, especially in the species growing in running water. Reproduction is effected by means of akinetes, 4-ciliate (and 2-ciliate?) zoospores, and by means of isogamous biciliate gametes. The zygospores in some cases germinate immediately. The ordinary cells function as sporangia and gametangia, producing large numbers of swarmers which escape by a lateral aperture.

[1] Fritsch, 1922, p. 1 et seq.

[2] Journ. Roy. Sanitary Inst. xxxiv, 1913, p. 465.

[3] *Pleurococcus vulgaris* Menegh. (non Naegeli) is a member of Prasiolaceae and possibly a form of *Prasiola* (cf. p. 211).

[4] Carter, Ann. of Bot. xxxiii, 1919, p. 467.

Chaetomorpha Kützing, 1845[1]. Filaments unbranched, attached at the base, of more or less uniform thickness, the lower cells being shorter than the upper ones. Cells broad, often slightly swollen, with thick firm and obviously lamellose walls. Reprod. by akinetes, differing but little from the ordinary vegetative cells, 4-ciliate zoosp., and 2-ciliate isogametes.

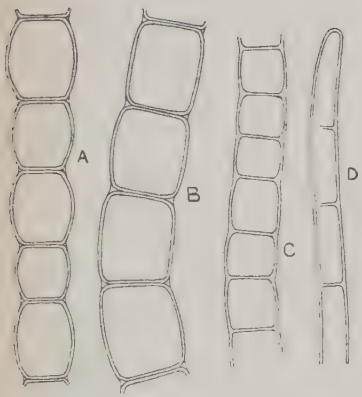

Fig. 62. *Chaetomorpha Linum* (Müll.) Kütz., from Heaton, W. Yorks (×100).

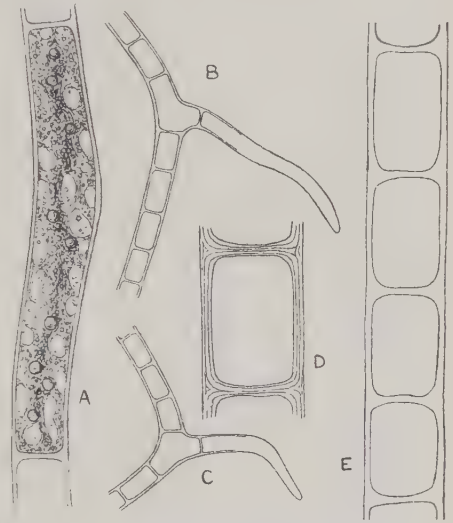

Fig. 63. A, *Rhizoclonium hieroglyphicum* Kütz., single cell showing chloroplast and pyrenoids, from Sheep's Green, Cambridge (×500). B–E, *R. hieroglyphicum* Kütz. var. *tortuosum* (Kütz.) Stockm., from Heaton, W. Yorks; B and C, ×100; D and E, ×500.

Most of the sp. are marine or frequent brackish water, but *C. Linum* (O. F. Müll.) Kütz. (*C. sutoria* Rabenh.) (fig. 62) is sometimes found in wells and horse-troughs, or in streams; filaments 100–120 br. Heering (1921, p. 16) regards this sp. as a form of *C. aerea* Kütz.

Rhizoclonium Kützing, 1843[2]. Filaments usually relatively narrow, with elongate cylindrical cells, at first attached by a branched basal hapteron; filaments frequently with short, slightly attenuated branches (often arising where the main thread is bent), sometimes merely unicell., but more commonly

[1] Lagerheim, Ber. Deutsch. Bot. Ges. v, 1887, p. 195.

[2] Gay, 1891, p. 23; Gay, Journ. de Bot. v, 1891, p. 53; Wille, Vidensk. Selsk. Skrift., Christiania, Mat.-nat. Kl., 1900, No. 6, p. 34; Brand, Bot. Centralbl. LXXIV, 1898, p. 193; Stockmayer, Verhandl. Zool.-Bot. Ges., Wien, XL, 1890, p. 571; Peterschilka, loc. cit.; Heering, 1921, p. 19.

consisting of several cells. Cell-walls firm, lamellose, and sometimes thick; cells often contain but few nuclei, occasionally only one. In autumn the cells are commonly packed with starch and enter upon a kind of resting-stage; by subsequent fragmentation multiplication may be effected. 2-ciliate zoosp. also recorded.

Stockmayer has given a good systematic account of this genus, the sp. of which are marine, brackish, freshwater, or may even occur on damp soil. The only Brit. freshw. sp. is *R. hieroglyphicum* Kütz. emend. Stockm. (*Conferva fontinalis* Berk.; *Microspora fontinalis* De Toni) (fig. 63, A), whose filaments are 10–37 br.; the cells 2–5 times as long. The common form of this sp. possesses no branches whatever and occurs abundantly as a perennial in ponds, ditches, drains, streams, and cataracts all over the country, thriving well in water in which considerable putrefaction is taking place. Widely distributed vars. are: var. *tortuosum* (Kütz.) Stockm. (fig. 63, B–E) with cells 26–40 br.; and var. *riparium* (Harv.) Stockm. with threads which are frequently bent and composed of cells (14–32 br.) with thick walls.

Cladophora Kützing, 1843[1] (incl. *Aegagropila* Kützing, 1849). Filaments typically richly branched, the type of branching varying in different sp. and its extent depending on the season and the condition of the plant. Branches nearly always arising from the upper end of a cell, just beneath a septum, and at first placed more or less at right angles to the parent-cell; sooner or later, however, by surface-growth of the latter, the branch becomes upwardly displaced (so-called "evection") and subsequently lies on the same level as the continuation of the main axis, so that an appearance of dichotomy or trichotomy results; fusion of branches at the base is also not uncommon. Cells elongate, 6–12 (or even up to 20) times as long as wide, with thick and distinctly stratified walls in which an inner and an outer zone and a superficial lamella (separated by treatment with acetic acid) are distinguishable. Growth in length of the different branches is practically restricted to the apical cell which, when it has reached a certain size, undergoes div. into two by the gradual ingrowth of a septum originating only from the inner layers of the longit. walls. Especially in the neighbourhood of the septa the inner lamellae of the wall are prominently folded, whereby joints are created contributing to the flexibility of the otherwise rather rigid threads. Basal attaching cell generally well developed, often aided in older plants by rhizoids which

[1] Berthold, 1878, p. 182; Gay, 1891, p. 14; Brand, Bot. Centralbl. LXXIX, 1899, p. 145; ibid., Beihefte, X, 1901, p. 481; Beihefte, XVIII, 1904, p. 165; Hedwigia, XLV, 1906, p. 241; Ber. Deutsch. Bot. Ges. XXIV, 1906, p. 64; ibid. XXVI, 1908, p. 114; ibid. XXVII, 1909, p. 292; Hedwigia, XLVIII, 1909, p. 45; Nordhausen, Jahrb. Wiss. Bot. XXXV, 1900, p. 366.

originate from the cells above and sometimes grow downwards through the lamellae of the wall. Reprod. is effected by akinetes, 2- or 4-ciliate zoosp., and by 2-ciliate gametes; the reprod.

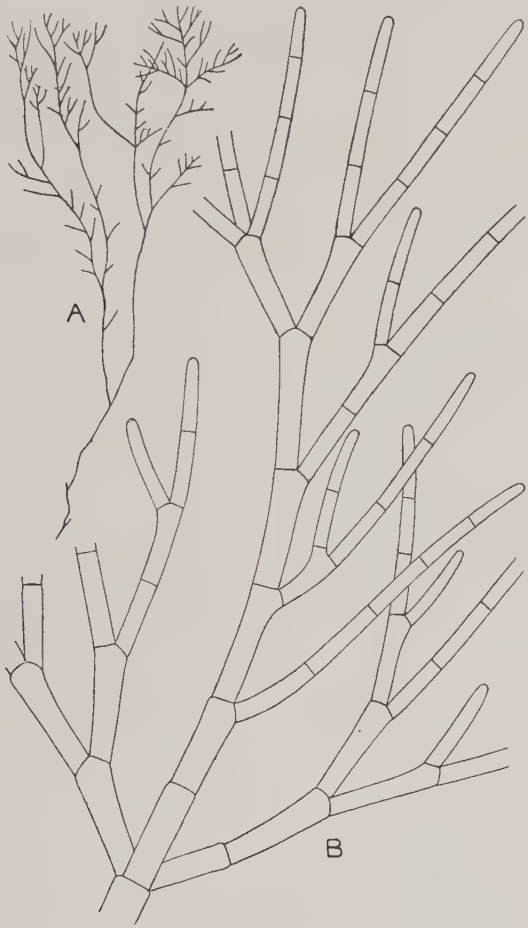

Fig. 64. *Cladophora glomerata* (L.) Kütz., from Shipley, W. Yorks. A, nat. size; B, ×85.

elements are mainly formed in the cells of the finer branches. The zygosp. germinates immediately.

Most of the sp. are marine, but a number occur commonly in freshwater. They are not easily distinguished from one another, except when typically developed. Brand, who devoted much time to a study

of the freshwater forms of *Cladophora*, recognises in the main three sp. *C. glomerata* (L.) Kütz. ampl. Brand (fig. 64) is a common form occurring as dark green masses attached to rocks and stones in streams and waterfalls; the main thread is anchored by a well-developed hapteron, the branching is dense with the finer branches often in tufts, apparent dichotomy is frequent, and the branches are often fused at the base. *C. crispata* (Roth) Kütz. ampl. Brand is another common sp., usually occurring attached to stones; it is distinguished from *C. glomerata* by the long, little ramified ultimate branches, the scarcity of apparent dichotomy, and the occurrence of basal fusions only in the oldest parts of the plant. *C. fracta* Kütz. ampl. Brand is a free-floating sp., of frequent occurrence in ponds and ditches, in which the process of evection, by contrast with the other two, takes place slowly and apparent dichotomy (or trichotomy) is only seen in the older parts of the plant. Of these different sp. Brand distinguishes a large number of diverse forms and states (status hiemalis, status ramosus, status simplicior, etc.), all of which he has clearly described[1].

In a number of sp. of *Cladophora* placed in the section *Aegagropila* (regarded by some as a separate genus) the plants grow in dense communities, forming compact cushions attached to some substratum or sometimes free-floating hollow balls which may become as big as a human head[2]. The plants are richly branched, are in the main placed at right angles to the surface of the cushion or ball, and the innermost parts gradually die, whereby the branches become separate, although they remain bound together by means of interweaving rhizoids. Such growths are mainly found on the floor of relatively shallow lakes. Two sp. of this section, viz. *C. holsatica* Kütz. and *C. Sauteri* (Nees) Kütz. are known from the English lakes, while the latter is also recorded from Hickling Broad; Acton[3] has recently given an account of the "balls" of the former. No swarmers have been observed in the sp. of *Aegagropila* which appear to multiply by vegetative means only.

Pithophora Wittrock, 1877[4]. Richly branched filaments with the habit of a *Cladophora*, from which the genus may be distinguished by the usually much thinner walls and the origin of the branches a little way below a septum (a condition only found rarely in *Cladophora*); the plants are attached by well-developed basal haptera. Reprod. is effected by characteristic akinetes; in their formation the greater part of the protoplast contracts

[1] Brand's results are well summarised in Heering, 1921, p. 26 et seq.

[2] cf. Brand, Hedwigia, XLI, 1902, p. 34 and XLV, 1906, p. 247; Wesenberg-Lund, Overs. K. Dansk. Vidensk. Selsk. Forhandl., 1903, No. 2, p. 167.

[3] Acton, New Phytol. XV, 1916, p. 1.

[4] Wittrock, Nov. Act. Reg. Soc. Sc., Upsala, ser. 3, 1877; Rendle and W. West jun., Journ. of Bot., 1899, p. 289; Moebius, Ber. Deutsch. Bot. Ges. XIII, 1895, p. 356; Ernst, Ann. Jard. Bot. Buitenzorg, 2 sér. VII, 1908, p. 18.

towards one end (usually the upper) of the cell, becomes cut off from the rest by a septum, and subsequently produces a thick wall; the akinetes are either intercalary and cask-shaped, or

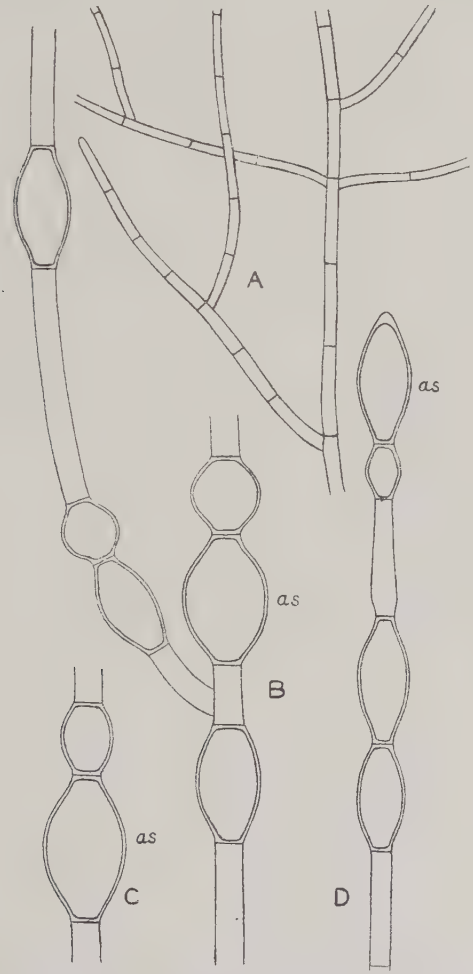

Fig. 65. *Pithophora Oedogonia* Wittr. var. *polyspora* Rendle and West, from the Reddish Canal, near Manchester. A, ×65; B–D, fragments of thallus with akinetes (*as*), ×100.

terminal and ovoid or fusiform, and are sometimes formed in twos or threes. After a short period of rest they develop in opposite directions from the two extremities.

This striking genus is no doubt really tropical in its distribution, both the English records being introductions. *P. Oedogonia* (Mont.) Wittr. var. *polyspora* Rendle and West (fig. 65) is found in the Reddish Canal near Manchester. *P. Kewensis* Wittr. occurred in a tank in the Water-Lily House, Kew Gardens, being probably introduced from tropical S. America.

Chaetonella Schmidle, 1901[1]. Plants small, branched, almost microscopic, either free-floating or attached to the mucous coat

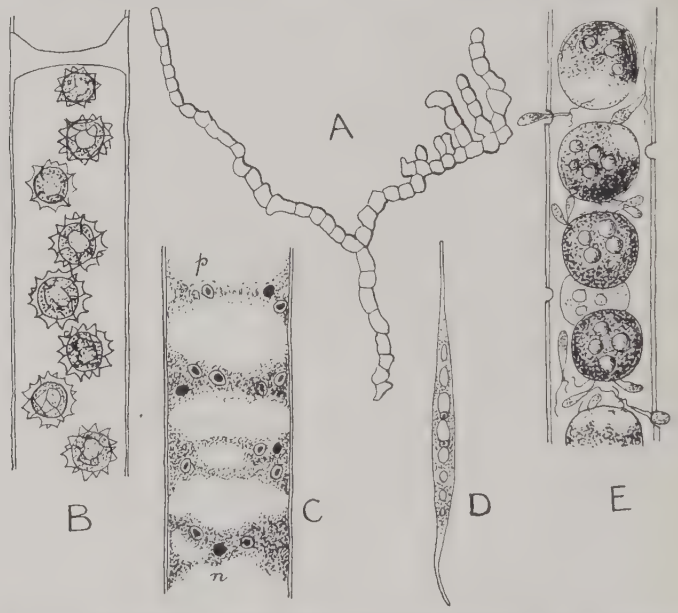

Fig. 66. A, *Chaetonella Goetzei* Schmidle (after Schmidle). B–E, *Sphaeroplea annulina* (Roth) Ag.; B, portion of cell with oospores, and C, portion of vegetative cell (after G. S. West, ×350); D, young filament formed from a zoospore (after Cohn, ×225); E, portion of oogonium showing ova and spermatozoids (after Cohn, ×350). *n*, nucleus; *p*, pyrenoid.

of larger Algae; branches attenuated, the terminal cells longer than the others. Cells cylindrical, or more or less irregular, each with 2–5 nuclei and a parietal chloropl. without pyrens. Reprod. by zoosp. (?) formed in some numbers in the middle cells of the threads.

The only sp., *C. Goetzei* Schmidle (fig. 66, A), is known from Tropical Africa and W. Yorks, where it was found epiphytic on *Spirogyra* (West and West, 1903, p. 38); cells 6–8 br. It is possible that this is really a member of the Chaetophorales.

[1] Schmidle, Engler Bot. Jahrb. xxx, 1901, p. 253.

Series IV. SPHAEROPLEALES

This includes only the family Sphaeropleaceae with the single genus

Sphaeroplea Agardh, 1824[1]. Filaments cylindrical, unbranched, free-floating, composed of a row of cylindrical coenocytes which reach an extraordinary length as compared with their breadth and are separated by transv. walls, often of great thickness and occasionally incomplete. Each segment contains a considerable number of small nuclei and several parietal annular chloropl.[2], each with several pyrens. (fig. 66, C).

Reprod. is effected by fragmentation and by an oogamous sexual process, the filaments being monoecious or dioecious, and the ordinary segments acting as oogonia or antheridia without change of shape; numerous ova and still more numerous spermatozoids are produced. Ova spherical, green, with a conspicuous receptive spot (fig. 66, E); sperms small, spindle-shaped, 2-ciliate, red-coloured. Small apertures are formed in the walls of the gametangia for the escape of the sperms and the fertilisation of the ova (fig. 66, E). Oospores remaining enclosed within the oogonia, with a thick verrucose wall and bright red contents (fig. 66, B). On germination they liberate 2–8 biciliate oval zoosp., which come to rest without seeking a substratum, so that the filaments to which they give rise are free-floating from the first. The young threads are fusiform with each extremity attenuated to a very fine point (fig. 66, D). An asex. method of propagation by zoosp. is highly probable, but is as yet unrecorded.

S. annulina (Roth) Ag. occurs extensively on inundated portions of the plains of Europe, Asia, and America, and is sometimes found in pits or quarries. Apart from its occasional occurrence in tanks in Kew Gardens (cf. Fritsch, 1906, p. 198), where it is probably introduced with various aquat. plants, it has been found by Prof. Lloyd Williams in pools between sand-hills at Morfa Bychan, S. Carnarvonshire; filaments 36–72 br.; segments up to 90 times as long (fig. 66, B–E). A second sp. has recently become known from S. Africa.

[1] Cohn, Ann. Sci. Nat., Bot., 4 sér. v, 1856, p. 187; Heinricher, Ber. Deutsch. Bot. Ges. 1, 1883, p. 433; Klebahn, Festschr. f. Schwendener, Berlin, 1899, p. 81; Fritsch, 1918, p. 524.

[2] Earlier accounts have spoken of numerous discoid chloroplasts, some with and some without pyrenoids and densely arranged to form transverse bands. Stained preparations of Dr Nellie Carter's, which she has kindly permitted me to examine, however show that each annular band constitutes a single chloroplast.

GROUP 4. CHAETOPHORALES

There is a fundamental difference between the organisation of the Chaetophorales and that of the Ulotrichales, plain enough in the more typical representatives of the three families Chaetophoraceae, Trentepohliaceae, and Coleochaetaceae, but obscured or almost unrecognisable in the numerous specialised forms that belong to this group. This outstanding characteristic lies in the differentiation of the vegetative body into a prostrate system of branching threads attached to some substratum and a projecting system likewise composed of branching filaments[1]. The two parts of the thallus are easily distinguished in many species of *Stigeoclonium* (fig. 2, II, p. 29), *Gongrosira* (fig. 78, F), *Trentepohlia*, and *Coleochaete*, whilst a reduction of the projecting system has given rise to a whole host of prostrate and discoid types. In the Ulotrichales, on the other hand, no such differentiation exists and prostrate types are unknown. In other respects also the Chaetophorales betray a high development, as for instance in the elaborate threads of *Draparnaldia* (fig. 70), the advanced oogamy accompanied by a kind of "fruit" formation in *Coleochaete* (fig. 68), the high degree of adaptation of the *Trentepohlias* to a terrestrial existence, etc. In no other group of the Isokontae do we find such a diversity of growth-forms. It is not impossible that the Chaetophorales represent the present-day descendants of forms from which the higher land-plants arose in the remote past (Fritsch, loc. cit.).

The principal characteristic of the Chaetophorales is not implied in the name which refers to the formation of "hairs." It is well to realise, however, that in the European Trentepohliaceae hairs are altogether lacking, and that under this name are comprised at least two perfectly distinct kinds of structures. In the Chaetophoraceae the hairs are single cells or rows of cells with scanty colourless contents (figs. 75, 76), whereas in the Coleochaetaceae (fig. 68, A) and Chaetopeltidaceae (figs. 84, 85) they are outgrowths of the wall (bristles or setae)[2]. They are therefore not a distinctive feature of the group, and one may well be going astray in including certain simple seta-bearing forms (Chaetopeltidaceae) in the same group with the others (cf. p. 181). It is however impossible to gauge how far the process of reduction has gone within the Chaetophorales.

An affinity of the less specialised types with the Ulotrichaceae is plainly recognisable, both in the cell-structure and in the

[1] Fritsch, New Phytol. xv, 1916, p. 235 et seq.
[2] cf. Huber, Journ. de Bot. vi, 1892, p. 321.

reproductive processes. The filamentous Chaetophorales are however practically always branched. The central type is constituted by *Stigeoclonium* (*Myxonema*), in many "species" of which both prostrate and projecting systems are well developed (fig. 2, H). Each cell, except those forming the hairs, contains a single parietal plate-shaped chloroplast with one or more pyrenoids.

In *Draparnaldia* the prostrate system may be altogether absent, but the projecting part is strikingly differentiated into long and short branches (fig. 70, A). The former consist of large, slightly barrel-shaped cells with a small chloroplast, having deeply incised edges and often forming merely an equatorial girdle in the otherwise colourless cell (fig. 70, B). The short branches arise in dense, frequently more or less whorled tufts, are richly branched and composed of short cells occupied by a large generally entire chloroplast similar to that of *Stigeoclonium*. The development of reproductive cells, and no doubt also the main assimilatory activity, are restricted to the short branches, the long ones being chiefly supporting in function (Berthold, 1878, p. 202). In no other Green Alga is there such a marked division of labour.

Both in *Stigeoclonium* and *Draparnaldia* the threads are usually embedded in thin mucilage, but in *Chaetophora* they are held together within a compact mucilage-envelope to form more or less globular or branched foliaceous masses. These (fig. 71, A and C) are readily visible to the naked eye, whilst the individual filaments are only discernible under the microscope. The projecting threads, which arise from a prostrate system composed of often almost separate rounded cells, branch more or less abundantly towards their tips. In all three genera, which appear closely allied, the apices of the branches are either pointed or drawn out into more or less long hairs, and in many cases at least the type of apex developed seems to depend on outside conditions.

In these three genera (often grouped as Chaetophoreae) a great diversity of swarmers has been observed, viz. (*a*) macrozoospores with four cilia in all three genera (figs. 69, B, D; 70, C), (*b*) microzoospores with four cilia in *Stigeoclonium* and *Draparnaldia*, (*c*) gametes with four cilia in the same two genera, and (*d*) gametes with two cilia in *Stigeoclonium* (fig. 69, C) and *Chaetophora*. *Draparnaldia* thus only produces tetrakontan swarmers; in *Stigeoclonium* and *Chaetophora* the normal zoospore is tetra-, the normal gamete di-kontan, so that there is a mingling of the two types as in *Ulothrix*. Pascher's *Iwanoffia*[1] is a

[1] Pascher, Bibl. Bot. LXVII, 1907, p. 63.

terrestrial *Stigeoclonium* in which only dikontan swarmers have become known. The formation of swarmers generally takes place simultaneously in a large number of cells; usually each cell produces only one or two of them and they are liberated through a lateral aperture in the wall (figs. 69, C; 70, C). The swarmers are evidently in a very plastic condition, the gametes in particular not being sharply defined from the microzoospores. Resting-cells are developed in many different ways, viz. by the formation of 1–4 aplanospores within a cell, by akinetes (fig. 70, D), from the microzoospores on cessation of movement, and lastly as a result of the isogamous sexual process (fig. 69, F). *Palmella*-like stages have also been observed, especially in *Stigeoclonium*[1].

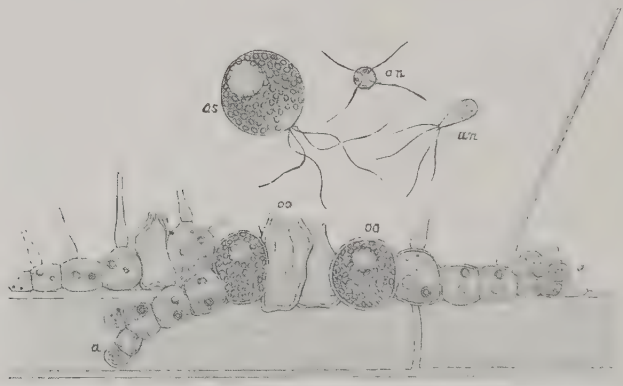

Fig. 67. *Aphanochaete repens* A. Br. *oo*, oogonium; *os*, ovum; *a*, antheridium; *an*, spermatozoid. (After Huber.)

The remaining genera of Chaetophoraceae are modified in various ways, the bulk of them being epiphytes on other water-plants. The tendency for reduction of the projecting system, evident in some species of *Stigeoclonium* (Berthold, 1878, p. 201), reaches its height in those Chaetophoraceous epiphytes, which either possess only a few projecting branches (*Chaetonema*, (fig. 74, A), *Pseudochaete* (fig. 75)), or nothing but hairs (*Aphanochaete* (fig. 76)), or have the projecting system completely suppressed (*Protoderma* (fig. 77), *Endoderma* (fig. 74, F)). Such forms may be conveniently grouped as Prostratae. The prostrate system often consists only of loosely branched threads, but in a number of genera these are compacted to form a 1-layered disc (*Trichodiscus*, *Protoderma*). In *Endoderma* (fig. 74, F) the threads grow beneath the superficial layers of the wall of Cladophoraceae,

[1] Cienkowski, 1876, p. 544.

etc. On the other hand, in a few forms (Erectae), it is the prostrate system that is lacking, as in the minute unbranched *Thamniochaete* (fig. 73) and the peculiar *Microthamnion* (fig. 72), whose exact systematic position is difficult to determine; in some respects it shows a (probably superficial) resemblance to Cladophoraceae. Another form of doubtful affinity is *Raphidonema* (fig. 74, E) which is like a septate *Ankistrodesmus* and a frequent member of certain snow-floras.

The reproduction of but very few of these specialised forms is at all well known, but the available data in the majority of cases indicate much similarity with what is recorded for *Stigeoclonium* and its immediate allies. *Aphanochaete* alone stands out by virtue of its marked anisogamy, amounting almost to oogamy. Oogonia are developed from enlarged globular cells devoid of hairs in the centre of the creeping filament (fig. 67, *oo*), and each gives rise to a single spherical 4-ciliate deep green macrogamete (*os*) containing a large and prominent oil-globule and liberated in the usual way. The small antheridia (*a*) are produced at the ends of the filaments, are frequently colourless, and give rise to one or two 4-ciliate pear-shaped microgametes (*an*). The latter exhibit active movement, whereas the macrogametes move little. The fate of the zygote is unknown. Many authorities place *Aphanochaete* in a separate family, but its anisogamy is so plainly derivable from the isogamy of other Chaetophoraceae that this appears unnecessary.

A second series of forms, in which hairs are only rarely developed, appears to have undergone less reduction, the majority of the Trentepohliaceae possessing a thallus with both prostrate and projecting systems. The members of this family produce their swarmers in sporangia or gametangia which are more or less sharply differentiated from the vegetative cells (figs. 78 and 80). They also show specialisation in other directions, to wit the frequent incrustration with carbonate of lime in *Gongrosira*, the capacity for penetrating into calcareous (e.g. shells of Molluscs) and other substrata in *Gomontia* (fig. 79, C, D), and the wind-dispersal of the sporangia in the terrestrial *Trentepohlia*. In *Gomontia* the prostrate system occupies the surface of the substratum, while the threads of the projecting system penetrate into it. The haematochrome, found in the cell-sap of the *Trentepohlias* and to which their frequent orange colour is due, is probably a protection against the strong light to which these forms are often exposed in their terrestrial habitat.

In *Gongrosira* (fig. 78, D and E) the sporangia are flask-shaped structures arising terminally on the projecting threads, whilst in *Gomontia* they are large irregularly swollen cells of the prostrate

system. In *Gomontia* they give rise to biciliate swarmers of two sizes which are believed to be gametes. In *Trentepohlia* (fig. 80) the spherical sporangia are again borne on the upright threads, the underlying cell often having a characteristic hook- or knee-shaped form (cf. p. 200). These sporangia usually become detached as a whole (cf. fig. 3, B, C) and distributed by the wind, liberating numerous quadriciliate (or sometimes biciliate?) zoospores only after subsequent contact with moisture. The gametangia of *Trentepohlia* are commonly found on the basal parts of the thallus and are spherical cells devoid of a stalk; the isogamous gametes are biciliate but resemble the zoospores closely, and it would seem that in many cases they germinate without fusion (see also p. 200).

In some species of *Trentepohlia* the upright system is strongly reduced; in fact the ordinary condition of *T. umbrina* is that of a number of very loosely connected cells forming a prostrate branch-system. A similar, but more extreme, reduction of some member of Chaetophorales may well have afforded the familiar *Pleurococcus* (*Protococcus*) (fig. 86), whose exact relationship is altogether obscure and certainly not with the *Trentepohlia*-group. Another reduced type, evidently related to *Trentepohlia*, is the epiphyllous *Phycopeltis* (fig. 79, B), forming greenish or orange-coloured specks on the leaves of *Abies*, *Hedera*, *Rubus*, etc. and not yet recorded for this country. Here the thallus consists almost entirely of the prostrate system which forms a 1-layered disc composed of radiating threads with cells containing haematochrome; sporangia are formed at the ends of short upright threads, whilst the gametangia are developed directly from the cells of the disc.

In classing the Gongrosireae and Trentepohliceae in the same family, the writer is reverting to a practice which Wille had abandoned[1]. In spite of the obvious differences between the two sets of forms, seen also in the cell-structure (Gongrosireae with one, Trentepohliceae with several chloroplasts per cell), they give the impression of a closer affinity than can be recognised for instance between the Gongrosireae and any of the true Chaetophoraceae, saving possibly *Microthamnion*. The difference of habitat is no longer so marked since Bristol has found a species of *Gongrosira* in the soil-flora, and there is much resemblance between the sporangia of the two sets of forms, although those

[1] Wille (1909, pp. 82, 84) includes the forms here placed in Gomonticae and Gongrosireae in Chaetophoraceae. Oltmanns (1922, p. 303), West (1916 *a*, p. 300), and Heering (1914, p. 102) do much the same. The classification here advocated is more on a line with that proposed by Blackman and Tansley (1903, p. 41).

of the Trentepohlieae are more highly developed. The inclusion of *Gomontia* in this family will rouse more opposition, but the arguments for its inclusion are of the same character. The alternative is to put it in a family of its own (together with *Tellamia*)[1], as many have done.

Coleochaete (fig. 81), occurring as discs or cushions commonly attached to water-plants, is a puzzling form around which many theoretical discussions have centred. It appears to be a remnant, like *Sphaeroplea* among Ulotrichales and *Vaucheria*

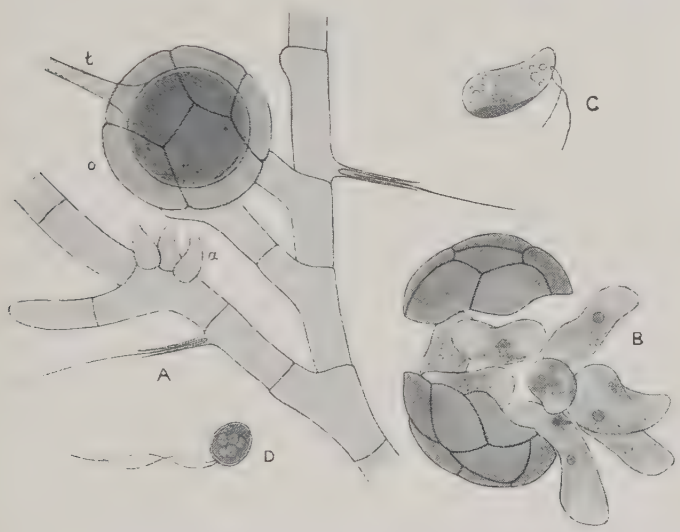

Fig. 68. *Coleochaete pulvinata* A. Br. A and B, from near Glenties, Donegal, Ireland. A, portion of thallus with sexual organs (×460); *o*, fertilised oogonium; *t*, "trichogyne"; *a*, antheridia. B, ripe "fruit" emitting the cells formed by the division of the oospore (×460). C, zoospore formed from the latter (after Chodat). D, zoospore produced from thallus (after Pringsheim).

among Siphonales, whose immediate allies have been wiped out. The peculiar sheathed setae (fig. 68, A), produced by many of the cells, have no parallel elsewhere, save in a few of the reduced Chaetopeltidaceae (cf. below). Nevertheless, in *C. pulvinata* A. Br. we have again a thallus with well-developed prostrate and projecting systems and in other species (*C. soluta*, *C. scutata*) a complete suppression of the latter and the assumption of a discoid pseudoparenchymatous habit (fig. 81). The two types of thallus-structure run parallel with what is encountered

[1] Acton (New Phytol. xv, 1916, p. 101) advocates an inclusion of this genus in *Endoderma*.

in Chaetophoraceae and Trentepohliaceae and they, as well as the simple plate-shaped chloroplast found in each cell, probably imply a remote affinity.

The isolation of *Coleochaete* is further emphasised by a consideration of its sexual reproduction. The oogonia (fig. 68, *o*) are enlarged cells of the projecting threads when these are present, or of the discs in the prostrate species; in the former case they develop a long neck (*t*) probably serving, like the trichogyne of Florideae, to facilitate reception of the male gamete; in the latter case they bulge in a hemispherical manner. The spermatozoids, which in the majority of the species are colourless, penetrate through an aperture formed in the oogonial wall—at the tip of the neck, when that is present. After fertilisation branches grow up around the oogonium from the adjacent cells (only on its outer surface in the discoid species) and form a complete 1-layered investment (fig. 68, A); the thick brown membrane of the oospore is formed, according to Oltmanns, by thickening of the wall of the oogonium and of the inner membranes of the cellular investment. In the possession of the latter *Coleochaete* is unique among Isokontae, although such fruit-formation is common enough in the Red Algae. When the oospore germinates, the contents undergo subdivision into 16 or 32 cells, whereupon the envelope is burst (fig. 68, B) and each cell produces a zoospore (fig. 68, C), differing considerably from the type formed in asexual reproduction by the ordinary thalli.

The mass of cells formed within the oospore, which is morphologically though not cytologically a sporophyte (since reduction occurs at the first division in the oospore)[1], is a further peculiarity of *Coleochaete*, although hinted at in the germination of the sexually produced spores of other Isokontae (e.g. *Ulothrix*, *Oedogonium*). The resemblances between the reproductive processes of *Coleochaete* and some Florideae are more apparent than real. In both cases we have a high degree of specialisation, and the similarities are no doubt an expression of the general trend which evolution in the lines of algal descent has followed. As regards the relationship between Chaetophoraceae, Trentepohliaceae, and Coleochaetaceae, they obviously represent three divergent, but parallel lines which need not even have had a common filamentous ancestry, since divergence may have taken place before the filamentous habit had become established.

The sheathed setae of *Coleochaete*, although formed mainly as an outgrowth of the cell-wall, do contain a narrow central thread of cytoplasm. Similar setae are encountered in *Chaetosphaeridium* (fig. 84) and *Conochaete* (fig. 85), in the former often

[1] Allen, Ber. Deutsch. Bot. Ges. XXIII, 1905, p. 289.

attaining a very great length. These genera are to all intents and purposes loose clusters of unicellular individuals, isolated cells being not uncommon, and may rightly be regarded also as members of the Chlorococcales. They, however, give the impression of reduced forms and are more conveniently considered in relation to the Chaetophorales, the more so as *Chaetosphaeridium* occasionally shows plain evidence of derivation from a filamentous condition (see p. 207). Whether the possession of similar bristles implies any relationship with *Coleochaete* may be doubted.

A number of further genera are distinguished by the presence of setae devoid of a sheath. Such are *Polychaetophora* (fig. 83) and *Oligochaetophora* (fig. 82, F), of which the former at least shows a filamentous tendency. A third genus, of doubtful affinity with the two others, is the discoid epiphyte *Chaetopeltis* (fig. 82, D), plainly a member of Chaetophorales parallel with *Coleochaete*, *Protoderma*, *Phycopeltis*, etc. Still more doubtful is the peculiar *Dicranochaete* (fig. 82, A) with repeatedly forked bristles. The combination of all these seta-bearing forms in the one family Chaetopeltidaceae is a matter of convenience and may safely be allowed until more definite data as to their possible affinities are forthcoming.

The following scheme will serve for the identification of the British genera of the group:

A. Plant-body mostly branched, frequently bearing simple hairs composed of one or more colourless cells, without specially differentiated sporangia, aquatic; sexual process isogamous or a very simple form of oogamy — *Chaetophoraceae*

a. Plant-body readily visible to the naked eye, sometimes differentiated into prostrate and projecting systems, the latter generally well developed and usually terminating in simple uni- or multicellular hairs — *Chaetophoreae*

1. Filaments not surrounded by a compact mucilage-envelope, separately visible to the naked eye

* Thallus without marked differentiation between the main axes and branches, prostrate and projecting threads usually well developed — *Stigeoclonium*

** Thallus showing marked differentiation between elongate and much wider main axes and numerous tufts of short lateral branches, without prostrate base — *Draparnaldia*

2. Filaments surrounded by a compact mucilage-envelope within which they are more or less radiately disposed — *Chaetophora*

b. Plant-body small or very small, often only visible on microscopic examination, epi- or endophytic or rarely free-floating, with or without hairs of a simple type

1. Thallus composed solely of the projecting system *Erectae*
   * Threads extensively branched, at first epiphytic, later free-floating, no hairs *Microthamnion*
   ** Threads unbranched, of only 3–6 cells, epiphytic, with a terminal hair *Thamniochaete*
   *** Threads unbranched, of few cells, attenuated at either end, free-floating *Raphidonema*
2. Thallus composed in the main of the prostrate system, the projecting system being represented by a few branches or hairs only *Prostratae*
   * Thallus with a few projecting threads
     † Prostrate system not compacted to form a disc
       § Projecting threads usually branched and each cell bearing long hairs *Chaetonema*
       §§ Projecting threads unbranched, gradually attenuated *Pseudochaete*
     †† Prostrate system compacted to form a disc composed of radiating threads *Trichodiscus*
   ** Thallus without projecting threads, the prostrate system bearing hairs which are bulbously inflated at the base, simple oogamous sexual process *Aphanochaete*
3. Thallus composed solely of the prostrate system, without hairs
   * Thallus epiphytic, discoid, of branched radiating threads *Protoderma*
   ** Thallus epiphytic, central cells rounded, peripheral ones elongated and radiating *Ulvella*
   *** Thallus endophytic in the membranes of other Algae *Endoderma*

B. Plant-body branched, without hairs, usually differentiated into prostrate and projecting systems, with specially differentiated sporangia, aquatic or terrestrial; sexual process isogamous *Trentepohliaceae*

a. Usually aquatic, devoid of haematochrome, single chloroplast, forming small cushions *Gongrosireae*
1. Chloroplast without a pyrenoid, sporangia developed from any cell *Leptosira*
2. Chloroplast with a pyrenoid, sporangia usually terminal, cushions frequently encrusted with carbonate of lime *Gongrosira*

b. Threads penetrating calcareous substrata or dead algal cells, single chloroplast *Gomontieae*
Only British genus *Gomontia*

c. Terrestrial forms, often with haematochrome, several chloroplasts per cell, without pyrenoids *Trentepohlieae*
1. Thallus richly branched, generally with well-developed prostrate and projecting systems *Trentepohlia*
2. Thallus epiphyllous, discoid *Phycopeltis*[1]

[1] So far not recorded for Great Britain.

C. Plant-body a 1-layered disc or a convex cushion, composed of more or less closely aggregated branched filaments, many of whose cells bear sheathed setae, advanced oogamous sexual process *Coleochaetaceae*
Only genus *Coleochaete*

D. Reduced epiphytic or free-floating forms, in some cases unicellular, the cells bearing gelatinous setae of diverse type *Chaetopeltidaceae*[1]
a. Setae devoid of a basal sheath, simple *Chaetopeltideae*
1. Thallus discoid composed of angular cells, setae sometimes absent *Chaetopeltis*
2. Cells subglobose or ovoid, loosely aggregated, each with two or more long flexuose setae
* Free-floating, cell-wall thick and stratified, each cell with 8–12 setae *Polychaetophora*
** Epiphytic, cell-wall thin, each cell with 2–4 setae *Oligochaetophora*
b. Setae devoid of a basal sheath, repeatedly forked *Dicranochaeteae*
Only genus *Dicranochaete*
c. Setae provided with a basal sheath *Chaetosphaeridieae*
1. Each cell with a single seta *Chaetosphaeridium*
2. Each cell with several setae *Conochaete*

E. Unicellular, multiplying by vegetative division, and occasionally forming short branched filaments, terrestrial *Pleurococcaceae*
Only genus *Pleurococcus*

Family 1. CHAETOPHORACEAE

The members of this family are, with very rare exceptions, aquatic and have a branched filamentous thallus, which is either plainly differentiated into prostrate and projecting systems, or one or other of these is more or less completely suppressed. In most genera hairs, composed of one or more cells devoid of chloroplasts, are present. The ordinary cells possess a single parietal plate- or girdle-shaped chloroplast which often has a dissected margin and usually contains one or two pyrenoids; the cell-wall is generally thin. Reproduction is effected by akinetes, 2- or more commonly 4-ciliate zoospores, aplanospores, and by a sexual process which, except in *Aphanochaete*, is isogamous. The reproductive elements are formed with or without division from the contents of the ordinary vegetative cells (cf. however *Trichodiscus* and *Aphanochaete*).

[1] cf. also *Gloeochaete*, p. 494.

Sub-family 1. Chaetophoreae

Plant-body large, readily visible to the naked eye.

Stigeoclonium Kützing, 1843[1] (*Myxonema* Fries, 1825)[2]. Thallus filamentous, somewhat mucilaginous, branched, usually differentiated into a prostrate, often more or less moniliform or torulose, system attached to some substratum, and a projecting system whose cells are elongated: branches of the latter scattered, often more or less isolated and elongated, rarely developed in dense clusters, either terminating in a point or in long hyaline hairs. The projecting threads of adult plants frequently float freely in ponds and ditches. Reprod. by macro- and microzoosp. with four cilia, by isogamous gametes with two cilia, by akinetes (developed especially in the prostrate system), and aplanosp. Microzoosp. occasionally behave as gametes, whilst the 2-ciliate gametes often fail to fuse: zygosp. either smooth or stellate. The macrozoosp. are stated to germinate directly, whilst the microzoosp. usually give rise to resting-cells.

The sp. of *Stigeoclonium* are but very insecurely founded. Great variability exists as regards the relative development of prostrate and projecting systems, the degree of branching of the latter, and the extent of hair-development. In some forms the projecting, in others the prostrate, system would appear to be very much reduced, but whether such are really independent sp. or mere habitat-forms is uncertain. As regards the projecting system Klebs (1896, p. 401) has shown that the extent of branching depends on the intensity of illumination, whilst hairs are produced much more plentifully in standing than in flowing water. Heering (1914, p. 68) has done very useful work in attempting a classification of most of the known forms, based largely on the degree of development and the type of branching of the projecting system. In a few cases the threads of the prostrate system are endophytic in the external cell-walls of other aquatics. *Palmella*-stages have been recorded for various sp. and, according to Livingston (loc. cit.), can be artificially induced by immersion in solutions of relatively high osmotic pressure (incl. sea-water) or in dilute solutions to which certain

[1] Cienkowski, 1876, p. 537; Berthold, 1878, p. 193; Huber, 1892, p. 274; Hazen, 1902, p. 193 (sub *Myxonema*); Livingston, Bot. Gaz. xxx, 1900, p. 289 and xxxix, 1905, p. 297; Livingston, Bull. Torrey Bot. Club, xxxii, 1905, p. 1; Fritsch, Beihefte Bot. Centralbl. xiii, 1903, p. 368; Pascher, Flora, xcv, 1905, p. 95 and Archiv f. Hydrobiol. u. Planktonkunde, i, 1906, p. 433; Ström, Nyt Mag. f. Naturvidensk. lix, 1921, p. 9.

[2] *Stigeoclonium* was adopted as a "genus conservandum" at the International Bot. Congress, 1910.

stimulating metallic salts have been added. The palmelloid cells can germinate directly to form new plants.

Sp. of this genus are most commonly found in spring in slow-flowing waters or in springs and are readily recognised by their delicate attached branching threads. Frequent and fairly well established forms are: *S. tenue* Kütz. (fig. 69), with well developed, but not very

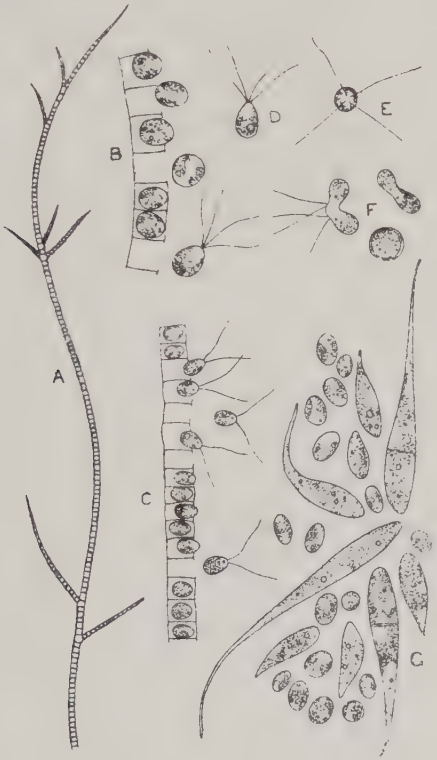

Fig. 69. *Stigeoclonium tenue* Kütz., from near the Lizard, Cornwall. A, part of thallus (×100); B, escape of zoospores; C, escape of gametes; D and E, zoospores; F, conjugation of gametes; G, germinating zoospores (×500).

extensively branched, projecting threads, the finer branches being both alternate and opposite; *S. lubricum* Kütz. which is abundantly branched, with the branchlets opposite or in pseudo-whorls; and *S. amoenum* Kütz. in which the branchlets of the projecting threads are usually opposite and mostly without hairs and the main axes are somewhat differentiated from the finer branches by the possession of thick-walled elongated cells with a meagre chloroplast. A var. of

S. farctum Berthold, one of the sp. in which the projecting system is much reduced, has been recorded from artificial waters in Kew Gardens (Fritsch, 1906, p. 200).

Draparnaldia Bory, 1808[1]. Thallus very mucilaginous, filamentous, without a prostrate system, the projecting one differentiated

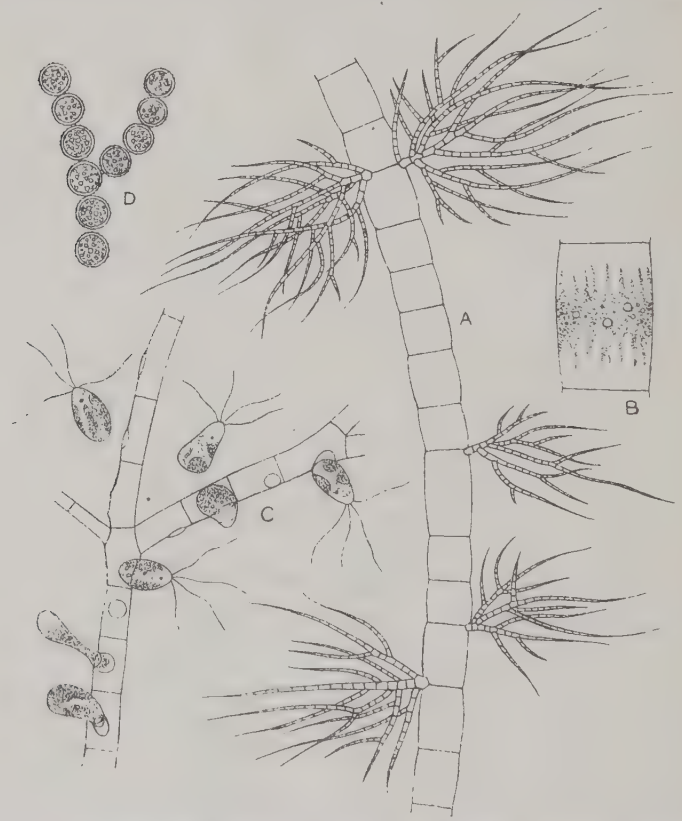

Fig. 70. *Draparnaldia glomerata* (Vauch.) Ag., from Tintagel, Cornwall. A, portion of thallus (× 100); B, single cell of main filament showing the chloroplast (× 220); C, part of branch showing escape of zoospores (× 500); D, akinetes formed from cells of branches (× 500).

into long and short branches; cells of long branches large, more or less barrel-shaped, with a scanty equatorial chloropl. with toothed edges and several pyrens.; short branches in clusters, alternate, opposite, or verticillate, richly branched, the apices

[1] Berthold, 1878, p. 202; Hazen, 1902, p. 217. The name of this genus is sometimes written *Draparnaudia*.

frequently tapering into long hyaline hairs, the chloropl. occupying nearly the whole length of the cells. Formation of reprod. elements confined to the short branches. Reprod. by 4-ciliate macro- and microzoosp., by aplanosp., and akinetes; swarmers (1–4 per cell) usually formed simultaneously throughout a cluster of branches, the entire process occupying only a few minutes and liberation taking place through a hole in the wall, often much smaller than the swarmer (fig. 70, C). Microzoosp. can act as gametes or give rise to resting-cells without fusion.

Two sp., *D. plumosa* (Vauch.) Ag. and *D. glomerata* (Vauch.) Ag. (fig. 70), are widely distributed in the Brit. Isles. They prefer clear water and occur both in bogs and amongst stones in streams, where they are usually found in quiet pools, stretching in long pale green gelatinous strands (up to 20 cm. long) from stone to stone. The lateral branches of *D. glomerata* are fewer and much shorter than those of *D. plumosa*, the cells are proportionately a little longer, and the hairs are also generally longer; diam. of long branches usually 40–50 μ, but sometimes considerably more; cells of short branches 5–10 br.

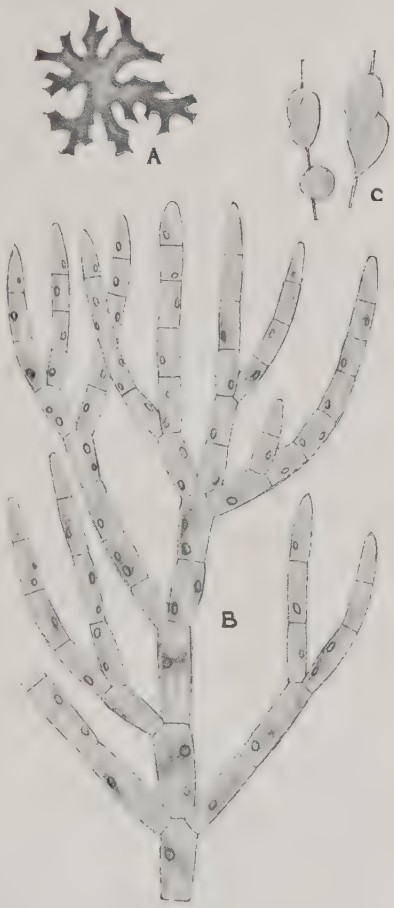

Fig. 71. A and B, *Chaetophora incrassata* (Huds.) Hazen, from Scarborough Mere, N. Yorks; A, nat. size; B, ×500. C, *C. elegans* (Roth) Ag., from Baildon, W. Yorks (nat. size).

Chaetophora Schrank, 1789[1]. Thallus a gelatinous macroscopic growth of definite form and of tough consistency, the component filaments being recognisable only on microscopic examination. Prostrate system feebly developed,

[1] Berthold, 1878, p. 210; Hazen, 1902, p. 209.

often of loosely connected rounded cells; filaments of projecting system radiating out from the base and at first little branched, but towards their apices bearing dense clusters of corymbose branches of a very bright green colour and with the terminal cells often prolonged into long hyaline hairs. Rhizoids may develop from some of the cells of older plants. Reprod. by brown-coloured akinetes, generally developed from the upper cells of the branches, by 4-ciliate zoosp. and 2-ciliate gametes.

Certain sp. (e.g. *C. incrassata*, *C. elegans*) have the power of precipitating calcium carbonate from the water in which they live and so giving rise to incrustations of considerable thickness[1].

The most abundant Brit. sp. is *C. pisiformis* (Roth) Ag., which occurs as hemispherical or almost spherical dark green masses attached to submerged stones and Phanerogams or the shells of aquatic Gastropods; it favours flowing water. It is distinguished by the absence of terminal hairs and the slightly torulose character of the cells of the branches; those of the main filaments are 9–15 br. The next most abundant sp. is *C. incrassata* (Huds.) Hazen (*C. endiviaefolia* Ag., *C. Cornu-Damae* (Roth) Ag.) with a tough gelatinous subdichotomously branched thallus, rather flat and of a darker green at the periphery than in the centre (fig. 71, A and B). Adult specimens are frequently found floating freely at the marshy margins of ponds and lakes, or even in bogs. *C. tuberculosa* (Roth) Ag. has a large cushion-shaped thallus, 2–5 cms. in diam. (with a tuberculate surface), and occurs usually in marshes or bogs. *C. elegans* (Roth) Ag. is rarer and is found as very pale green masses clinging to submerged stems and leaves of Grasses, Sedges, or Mosses (fig. 71, C); the thalli are often confluent and the ultimate branching of the threads is not as dense as in *C. pisiformis*.

Sub-family 2. Erectae

Plant-body microscopic, composed solely of the projecting system. It is doubtful whether the forms here included have any real affinity with one another.

Microthamnion Naegeli, 1849; Kirchner, 1878[2]. Thallus a well-branched filament (not exceeding 1 mm. in height), devoid of hairs, at first attached, later often free-floating; branches short or long, often unilateral, arising immediately beneath a septum and at first appearing as lateral outgrowths from the upper end of the parent-cell, the separating wall often formed

[1] A form of *C. elegans* showing this feature was named by Tilden (Bot. Gaz. XXIII, 1897, p. 102) *C. calcarea*, but the incrustation seems to constitute the only marked point of difference (cf. Hazen, 1902, p. 217).

[2] Borzi, Nuova Notarisia, II, 1891, p. 387; Schmidle, Hedwigia, XXXVIII, 1899, p. 165; Hazen, 1902, p. 190; Greger, Hedwigia, LVI, 1915, p. 374.

some distance up in the branch. Cells thin-walled, cylindrical, 3–7 times as long as broad, terminal cells obtuse or acuminate; chloropl. without pyrens., a long parietal plate occupying about two-thirds of the cell, often pale green, storing oil-drops. Reprod.

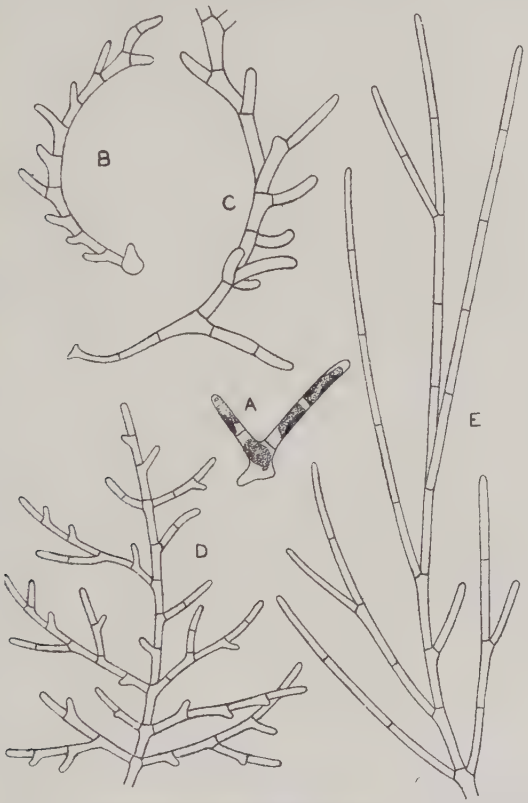

Fig. 72. A–D, *Microthamnion Kützingianum* Naeg. A–C, young forms from Richmond Park, Surrey (×500). D, portion of adult form from Horton-in-Ribblesdale, W. Yorks (×350). E, *M. strictissimum* Rabenh., from Blubberhouses, W. Yorks (×500).

by pear-shaped 2-ciliate zoosp., 4–8 (–32) of which are formed from any cell except the basal one[1]; thick-walled akinetes also recorded.

Of the two Brit. sp., *M. Kützingianum* Naeg. (fig. 72, A–D) is much more abundant, being found especially in the early spring in small

[1] The special terminal sporangia mentioned by Wille (1897, p. 97) and Blackman and Tansley (1903, p. 42) require confirmation (cf. also Hazen, 1902, p. 190).

pools and ditches; it likes peat. It is a small plant with many short branches of 1–6 cells (3–5 br.). *M. strictissimum* Rabenh. (*M. vexator* Cooke) (fig. 72, E) is larger, with much longer and more rigid branches, giving the plant a very different appearance from that of *M. Kützingianum*; cells 4 br.

Thamniochaete Gay, 1893[1]. Thallus epiphytic, a minute unbranched erect filament of 3–6 cells, the basal one being modified for attachment; terminal cell or cells with an elongated unicell. hair or a short spine-like projection. Chloropl. parietal, with one pyren. Reprod. by brown-coloured akinetes alone known.

T. aculeata W. & G. S. West (fig. 73) has been found as a rare epiphyte in the thallus of *Gloeotrichia natans* at Connemara in Ireland and in the Hebrides. The terminal cell is somewhat swollen and bears below its apex a short and very sharp bristle; cells 5·5–13 br. The other sp., *T. Huberi* Gay, is so far only recorded from France where it was found epiphytic on *Oscillatoria*; it gives the impression of reduction from a branched form.

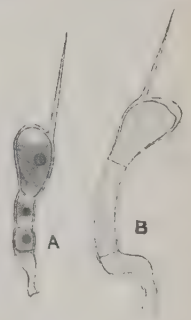

Fig. 73. *Thamniochaete aculeata* W. & G. S. West. A, from near Balallan, Outer Hebrides; B, from Baheh Lough, Galway, Ireland (×520).

Raphidonema Lagerheim, 1892[2]. Thallus an unbranched, unattached, often curved thread, usually tapering at each end and composed of a small number (4–7) of elongate thin-walled cylindrical cells. Chloropl. a parietal plate without pyrens. Reprod. by splitting of the thread into two.

R. nivale Lagerh. (fig. 74, E) has been recorded from near Settle in Yorkshire (West and West, 1901, p. 21); the cells are 4–6 br. The usual habitat is on the surface of snow. The view expressed in the first edition of this work (p. 80) as to its fungal nature was not subsequently maintained by G. S. West (1916 *a*, p. 287), nor is Wille's reference of *Raphidonema* to *Ankistrodesmus* generally accepted.

Sub-family 3. Prostratae

Thallus microscopic, composed in the main of the prostrate system; projecting system feebly developed or absent.

[1] Gay, Bull. Soc. Bot. France, xl, 1893, p. clxxvii; West and West, 1903, p. 38.

[2] Lagerheim, Ber. Deutsch. Bot. Ges. x, 1892, p. 523; Fritsch, Journ. Linn. Soc., Bot. xl, 1912, p. 317; Chodat, 1913, p. 165.

Chaetonema Nowakowski, 1876[1]. Thallus filamentous, epiphytic in the mucilage-envelopes of other Algae, composed of a little branched creeping system giving rise to short vertical projecting threads which are sometimes branched and each cell of which bears one or two long unicell. hairs slightly swollen at the base. Cells cylindrical, with a plate-shaped chloropl. with one or more

Fig. 74. A, *Chaetonema irregulare* Nowak. (after Huber, ×160). B–C, *Ulvella Beesleyi* Fritsch (after Beesley); B, mature thallus (×350); C, zoospores (×600). D and G, *Trichodiscus elegans* Welsford (after Welsford); D, small part of periphery of disc (×280); G, group of sporangia (*sp*) from centre of disc (×350). E, *Raphidonema nivale* Lagerh. (after Lagerheim). F, *Endoderma Cladophorae* Hornby (after Hornby, ×300), within the membrane of *Cladophora*.

pyrens., occupying the greater part of the cell. Reprod. by ovoid 4-ciliate zoosp., two formed from each cell. *Palmella*-stages, whose cells multiply by a kind of budding, also known.

C. irregulare Nowak. (fig. 74, A), the only sp., is a rare Alga recorded from W. Yorks, growing at the periphery of a *Palmella*-stage of *Chlamydomonas* (West, 1912, p. 328); cells 5–8 br. The genus is chiefly

[1] Nowakowski, Cohn's Beitr. z. Biol. d. Pfl. II, 1877, p. 75; Huber, 1892, p. 302; Huber, Bull. Herb. Boissier, II, 1894, p. 163.

distinguished from some of the reduced forms of *Stigeoclonium* by the presence of hairs on all the cells of the projecting threads; these hairs are probably to be regarded as reduced branches.

Pseudochaete W. & G. S. West, 1902[1]. Thallus filamentous, epiphytic, consisting of a (branched?) prostrate system of cylindrical or barrel-shaped cells, bearing narrower vertical unbranched threads which are composed of 5–8 much elongated cells and are attenuated to fine points. Chloropl. parietal, a pyren. only recognised in the cells of the prostrate thread; the last one or two cells of the upright threads may be devoid of contents. Reprod. unknown.

P. gracilis W. & G. S. West (fig. 75) is a rare epiphyte on aquat. plants; cells of creeping filaments 5·7–7·7 br. and $1\frac{1}{4}$–$2\frac{1}{4}$ times as long, those of the erect branches only 1·5–1·8 br. and 8–18 times as long. This Alga shows considerable resemblance to *Aphanochaete*, but differs in the possession of septate erect branches instead of simple hairs. The only other sp., *P. crassisetum* W. & G. S. West recorded from Ceylon, was regarded by G. S. West as possibly a developmental stage of *Stigeoclonium*.

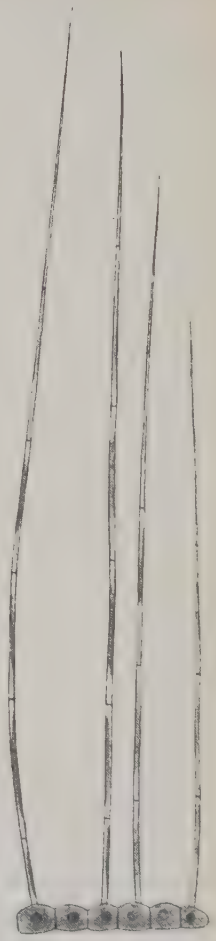

Fig. 75. *Pseudochaete gracilis* W. & G. S. West, from near Coates, Gloucestershire (× 520).

Trichodiscus Welsford, 1912[2]. Thallus discoid, about 1 mm. in diam., epiphytic; prostrate system composed of branched radiating threads coalescing to form a 1-layered disc, but free at the margin and there sometimes curving upwards; upright system consisting of numerous short, rarely branched, few-celled threads and scanty long septate hairs (usually found near the periphery). Chloropl. a lobed parietal plate with a single pyren. Reprod. by zoosp., 2-ciliate isogametes, and aplanosp.; the swarmers are formed in somewhat enlarged cells (fig. 74, G) of the upright threads. *Palmella*-stages also recorded.

[1] West and West, 1903, p. 37.
[2] Welsford, Ann. of Bot. xxvi, 1912, p. 239.

T. elegans Welsford (fig. 74, D, G) was found on the sides of a glass jar containing *Azolla Caroliniana* imported from N. Carolina and is therefore hardly to be regarded as a Brit. Alga. It is only distinguished from some of the reduced sp. of *Stigeoclonium* (e.g. *S. farctum*) by the development of special sporangia and gametangia, in which respect an affinity to Trentepohliaceae is indicated.

Aphanochaete A. Braun, 1851[1] (*Herposteiron* Naegeli, 1849)[2]. Plant a prostrate branched filamentous epiphyte, some or all of

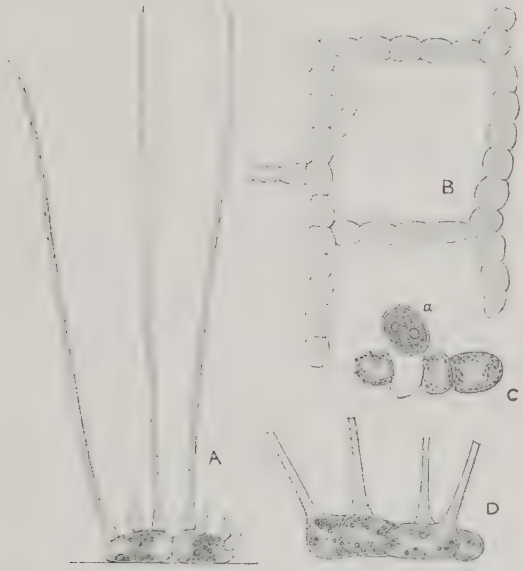

Fig. 76. A, *Aphanochaete polychaete* (Hansg.) Fritsch, from Wimpole Park, Cambridgeshire. B–D, *A. repens* A. Br.; B and C, from Bradford, W. Yorks; D, from Richmond Park, Surrey. (×450.) *a*, aplanospore.

the cells of which bear on the dorsal surface one or more erect unicell. hairs inflated at the base; in cultures these are sometimes replaced by branches[3]. The hairs at an early stage lose their protoplasmic contents; plugs of refractive substance often simulate transv. septa, but it has been conclusively shown that the hairs are single cells. Chloropl. single, parietal, with 1–2

[1] Braun, Betracht. üb. d. Erschein. d. Verjüng. i. d. Natur, 1851, p. 196; Huber, 1892, p. 278; Huber, Bull. Soc. Bot. France, XLI, 1894, p. xciv; Fritsch, Ann. of Bot. XVI, 1902, p. 403; Hazen, 1902, p. 229.

[2] cf. Nordstedt, Bot. Notiser, 1906, p. 118.

[3] Chodat, 1902, p. 324.

pyrens. Asex. reprod. by 4-ciliate zoosp.[1] of variable size and usually possessing an eye-spot; 1–4 are formed per cell, the wall rupturing to set them free. On coming to rest they generally develop unilaterally into a new plant. Aplanosp. sometimes formed (fig. 76, C).

The sex. reprod. (fig. 67) is of an oogamous type, but fertilisation takes place outside the plant. Globular oogonia (*oo*) develop by enlargement of some of the central cells which are devoid of hairs; the single female gamete (*os*) is 4-ciliate and is expelled by rupture of the wall. Antheridia (*a*), which are commonly almost colourless and considerably smaller than the vegetative cells, originate near the ends of the creeping branches and give rise to one or two spermatozoids each; the latter (*an*) are pear-shaped, provided with four cilia, a minute chloropl., and two contr. vacs., and are much smaller than the zoosp.; they are liberated into a hyaline vesicle which soon becomes diffluent. The spermatozoids exhibit active movement, but the female gametes are sluggish and come to rest prior to fertilisation. The further development of the thick-walled red-coloured oospores is unknown.

Sp. of this genus occur as epiphytes on *Cladophora*, *Rhizoclonium*, *Oedogonium*, and *Mougeotia*, as well as on the leaves, etc. of submerged Phanerogams. Well-developed specimens are much branched, the threads often following the contours of the cells of the substratum, so that a reticulum (fig. 76, B) may be produced. The hairs are easily broken off and frequently only their bases are present. The specific limits are not at all clear. The commonest sp. is *A. repens* A. Br. (*Herposteiron confervicola* Naeg.) which has oblong-ellipsoidal cells each bearing a hair; it is somewhat variable and two hairs are occasionally formed on some of the cells (figs. 67 and 76, B–D). *A. polychaete* (Hansg.) Fritsch (fig. 76, A) is abundant in some parts of the Brit. Isles; the cells are more ellipsoidal and possess from 1–4 hairs; *A. pilosissima* Schmidle only differs in the presence of a mucilage-sheath about the thread and prominent thickening of the wall in the bulbous base of the hair[2].

Protoderma Kützing, 1843; emend. Borzi, 1895[3]. Thallus epiphytic, a 1-layered pseudoparenchymatous disc, composed of a small central group of polygonal irregularly arranged cells with short branched filaments (sometimes a little attenuated) radiating from it; no erect branches or hairs. Chloropl. parietal,

[1] Pascher (Ber. Deutsch. Bot. Ges. xxvii, 1909, p. 143) has described a species in which these zoospores soon withdraw their cilia and exhibit amoeboid movement.

[2] cf. Schmidle, Hedwigia, xxxvi, 1897, p. 5, and xxxviii, 1899, p. 164.

[3] Borzi, Studi Algologici, ii, 1895, p. 245.

plate-shaped, with a single pyren. Reprod. by spherical or ovoid 2-ciliate zoosp., with eye-spot and two contr. vacs., 4–8 usually formed per cell and liberated by solution of the wall; also by aplanosp. *Palmella*-stages recorded.

P. viride Kütz. (fig. 77) is a not uncommon epiphyte on all kinds of submerged aquatics, both Algae and Phanerogams. G. S. West[1] regarded *Entocladia gracilis* Hansg. (*Endoderma gracile* De Toni) as referable to this Alga.

Ulvella Crouan, 1859[2] (incl. *Dermatophyton* Peter, 1886; *Epiclemydia* Potter, 1886). Thallus epiphytic, at first a 1-layered pseudoparenchymatous disc composed of radiating filaments which may or may not be distinct at the margin, later developing several layers of rounded cells at the centre; marginal cells often

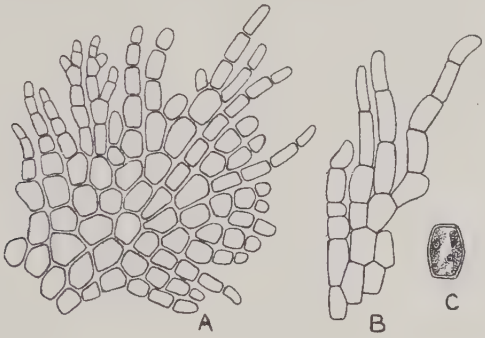

Fig. 77. *Protoderma viride* Kütz., from Baildon, W. Yorks, epiphytic on *Callitriche stagnalis*; A and B, parts of two plants, ×520; C, single cell, ×700.

forked; no erect branches or hairs. Chloropl. a parietal plate, without pyrens. Reprod. by 2-ciliate pear-shaped zoosp., formed from the central rounded cells and liberated by dissolution of the walls.

U. involvens (Savi) Schmidle is an epiphyte on the carapace of tortoises, but has not been observed in this country. It would seem, however, that an Alga described in 1904 by L. Beesley[3] belongs to this genus and may be given the name *U. Beesleyi* F. E. Fritsch (fig. 74, B, C); it formed green thalli on the surface of small sand-grains in some of the pools near Fleam Dyke, Cambridgeshire, where numerous small springs keep the sand-particles in active movement. The sp. differs principally from *U. involvens* in the fact that the component filaments are free from one another at the margin.

[1] West, Journ. of Bot., 1899, p. 58; West, 1904, p. 205.
[2] Huber, 1892, p. 294; Potter, Journ. Linn. Soc., Bot. XXIV, 1888, p. 251.
[3] New Phytol. III, 1904, p. 74.

Endoderma Lagerheim, 1883[1] (incl. *Periphlegmatium* Kützing, 1843, in part). Thallus endophytic in the cell-membranes of other Algae, composed of branched filaments which in some sp. coalesce to form a compact pseudoparenchymatous usually 1-layered stratum; no erect branches or hairs. Chloropl. a large parietal plate, with one or several pyrens. Reprod. by ovoid 4-ciliate zoosp. and ovoid 2-ciliate isogametes; the swarmers are formed in slightly enlarged cells (developing 2–8 zoosp., 6–16 gametes) and escape through an aperture in the wall.

Most sp. are marine. *E. Cladophorae* Hornby, endophytic in various Cladophoraceae, is known from the Midlands and is characterised by the coalescence of the branching filaments to form compact strata (fig. 74, F). A somewhat similar form was described by the writer[2] inhabiting *Cladophora* in the pond, Kew Gardens, Surrey.

Family 2. TRENTEPOHLIACEAE

The members of this family are partly aquatic (Gongrosireae) and partly terrestrial (Trentepohlieae) and in most the thallus is plainly differentiated into prostrate and projecting systems. Hairs are completely absent in the European forms. The cells contain either a single chloroplast with or without pyrenoids (Gongrosireae, Gomonticae) or several chloroplasts without pyrenoids (Trentepohlieae). Reproductive cells (zoospores or isogametes, the latter invariably biciliate) are produced in specially differentiated sporangia or gametangia; aplanospores are also known.

Sub-family 1. Gongrosireae

Mainly aquatic, forming small epiphytic cushions; chloroplast single; cells devoid of haematochrome.

Leptosira Borzi, 1883[3]. Thallus aquatic, forming very minute bright green cushions, composed of prostrate and projecting threads which are torulose with elliptical, doliform, or sometimes irregularly shaped terminal cells. Chloropl. pale yellow-green, without pyrens., but with scattered starch-grains; cell-wall thin. Reprod. by 2-ciliate swarmers produced in considerable numbers by simultaneous div. of the contents of any of the older cells which become but slightly enlarged and open by an aperture in the wall (fig. 79, A). Zoosp. and gametes not morphologically distinguishable, the latter fusing by their posterior ends to form a resting zygosp. Zoosp. stated to form a *Characium*-like stage

[1] Huber, 1892, p. 313; Hornby, New Phytol. xvii, 1918, p. 41.
[2] Fritsch, Beihefte Bot. Centralbl. xiii, 1903, p. 381, tab. XII, figs. 33–36.
[3] Borzi, Studi Algologici, i, 1883, p. 17.

whose contents give rise to 2–8 aplanosp. which are liberated by gelatinisation of the wall and produce new plants.

L. Mediciana Borzi (fig. 79, A), the only Brit. sp., is known from Yorkshire (West and West, 1901, p. 29), being found amongst *Sphagnum* and *Utricularia* in bogs and boggy pools; cells up to 20 br.

Gongrosira Kützing, 1843[1] (incl. *Stereococcus* Kützing, 1833; *Pilinia* Kützing, 1843, in part; *Ctenocladus* Borzi, 1885). Thallus

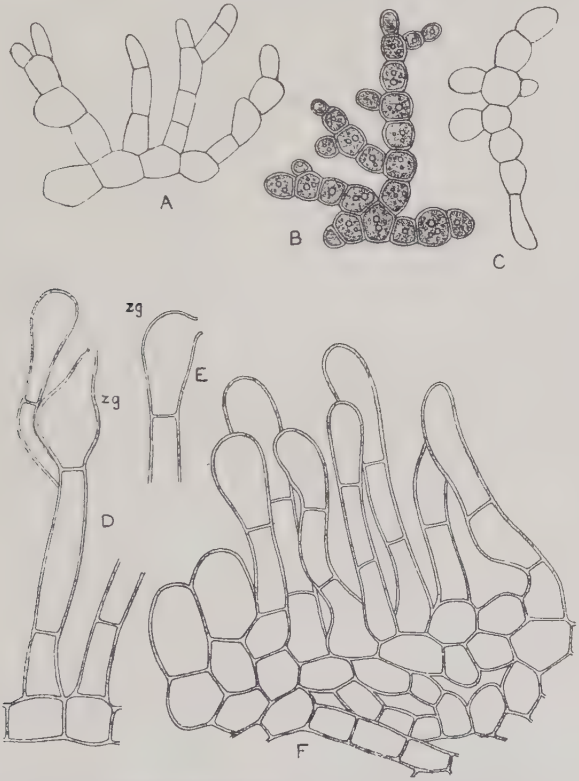

Fig. 78. A–C, *Gongrosira viridis* Kütz. (×500). A, from rocks, Lough Beg, Ireland; B and C, from rocks near Tremethick, Cornwall. D–F, *G. stagnalis* (West) Schmidle, from near Sutton, Cambridgeshire (×200). *zg*, zoosporangium.

usually aquat., generally attached to the substratum by a pseudoparenchymatous 1- or several-layered base, which is

[1] Wille, 1887, p. 484; Schmidle, Österr. Bot. Zeitschr. XLVII, 1897, p. 41; Schmidle, Ber. Deutsch. Bot. Ges. XIX, 1901, p. 10; West, 1912, p. 329; West, Journ. Roy. Microscop. Soc., 1918, p. 30.

formed by the confluence of the prostrate threads and bears numerous branched projecting threads from 0·04 to 2 mm. in height; the whole constituting a dense cushion-like mass frequently incrusted with carbonate of lime and sometimes forming quite a hard stratum (*G. Scourfieldii* West). Chloropl. a parietal plate with one or more pyrens., but usually ill-defined; cell-wall often thick and distinctly lamellose; cells frequently of irregular shape. Reprod. by (*a*) akinetes detached generally from the prostrate system, (*b*) ovoid 2-ciliate zoosp. formed in considerable numbers in special sporangia (fig. 78, D, E) which are often terminal and flask-shaped, though sometimes intercalary, and (*c*) 2-ciliate gametes which are imperfectly known.

The plants usually occur at the margins of ponds, lakes, or rivers forming a tough green stratum on submerged stones or on the shells of aquat. Gastropods. The sp., of which five have been recorded in the Brit. Isles, are grouped in two sections, viz. *Eugongrosira* in which the sporangia are much larger than the vegetative cells, and *Ctenocladus* in which they are scarcely enlarged. To the former belong: *G. viridis* Kütz. (fig. 78, A–C), a small sp. (primary filaments 8–12 br.; branches 4–8 br.), usually encrusted with lime; and *G. stagnalis* (West) Schmidle (fig. 78, D–F), which is larger (prim. fil. 16–30 br.) and occurs on the shells of *Limnaea peregra*. The section *Ctenocladus* includes: *G. Schmidlei* Richter, in which the projecting threads show unilateral branching and all the threads are of the same width (8–14), a chloropl. being mostly only present in the outermost cells; and *G. terricola* Bristol (1920, p. 77), the only terrestrial sp. known, which is characterised by the basal or intercalary position of its sporangia.

Sub-family 2. Gomontieae

Aquatic, penetrating calcareous substrata or dead algal cells; chloroplast single; cells devoid of haematochrome.

Gomontia Bornet et Flahault, 1888[1]. Thallus aquat., epiphytic, usually consisting of an often almost pseudoparenchymatous prostrate system developed on the surface and giving rise on the lower side to elongate projecting threads which penetrate deeply into the substratum, which may be calcareous, woody, or composed of dead algal cells; cells of irregular shape, those of the penetrating system often very long. Chloropl. parietal, of varied form (discoid, lobed, band-shaped, or reticulate), with one or several pyrens.; cells often with several nuclei. Reprod. elements formed in enlarged cells of the prostrate system which

[1] Bornet et Flahault, Journ. de Bot. II, 1888, p. 163, and Bull. Soc. Bot. France, XXXVI, 1889, p. clii; Wille, Vidensk. Selsk. Skrift., 1906, No. 3, p. 29; Acton, New. Phytol. XV, 1916, p. 97; Moore, Ann. Missouri Bot. Gard. V, 1918, p. 211.

often develop special attaching rhizoids of their own[1]; there have been distinguished (*a*) slightly enlarged zoosporangia producing 2–4 ovoid 4-ciliate zoosp., (*b*) much enlarged aplanosporangia producing numerous aplanosp., and (*c*) much enlarged gametangia (?) forming numerous pear-shaped 2-ciliate swarmers of different sizes whose sexual fusion is not yet established. Akinetes also known.

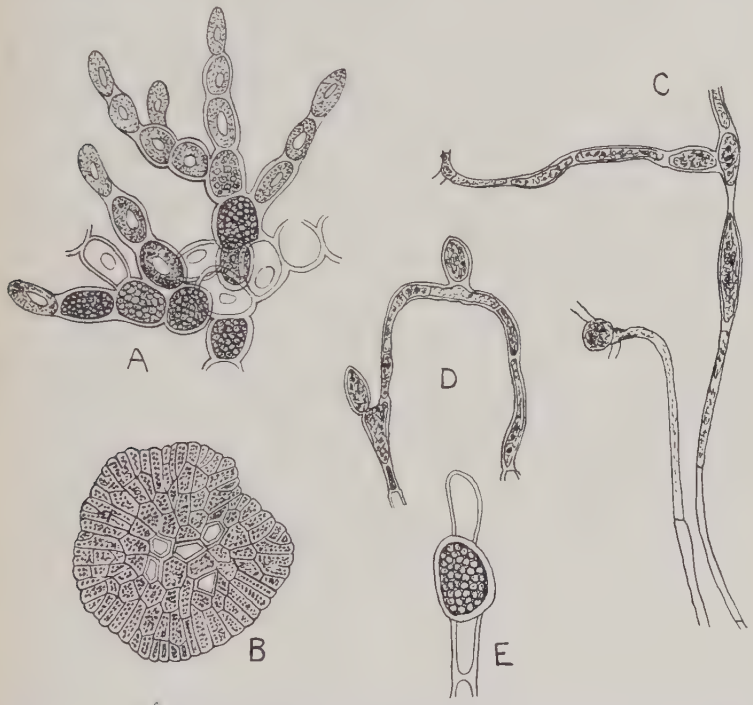

Fig. 79. A, *Leptosira Mediciana* Borzi (after Borzi, ×460); numerous sporangia seen in the lower part of the filament, some empty, others with divided contents. B, *Phycopeltis epiphyton* Millard. (after Millardet, ×225), showing a number of empty gametangia. C–E, *Gomontia Aegagropilae* Acton (after Acton); C and D, parts of penetrating system (×400); E, akinete (×645).

Several sp. of the genus are marine. The only freshwater sp., so far recorded in this country, is *G. Aegagropilae* Acton inhabiting the dead cells of *Cladophora holsatica* "balls" in Loch Kildona, S. Uist, Hebrides; the only method of reprod. observed was by means of akinetes, but zoosp. evidently also occur (fig. 79, C–E).

[1] These were first described by Lagerheim (Öfvers. K. Sv. Vet.-Akad. Förhandl. XLII, 1885, No. 8, p. 21) as a species of *Codiolum*.

Sub-family 3. TRENTEPOHLIEAE

Terrestrial; chloroplasts several, without pyrenoids; cells with haematochrome.

Trentepohlia Martius, 1817[1] (*Chroolepus* Agardh, 1824). Thallus aerial, usually orange-red or yellowish in colour, attached to rocks, tree-trunks, or wood-work, composed of prostrate and projecting systems, the latter sometimes much reduced; filaments richly branched, branches alternate and generally slightly attenuated, all of the same diam., growth mainly apical. Cells cylindrical, moniliform, or torulose, uninucleate or older cells with several nuclei; walls of cellulose, usually thick, stratified, with parallel or divergent layers, the free ends of the apical cells often covered by caps of pectose, transv. walls often with a single large pit; chloropl. numerous, discoid or band-shaped, without pyrens.; red or orange-red haematochrome usually present in the cell-sap.

Reprod. by akinetes set free by the breaking up of parts of the thallus, and by flattened or ovoid 2- or 4-ciliate swarmers formed in special ellipsoid or ovoid sporangia of three kinds. These are: (*a*) stalked sporangia (fig. 3, G), which arise terminally or laterally and are formed by the cutting off of a tubular outgrowth arising from the somewhat enlarged supporting cell, the septum developing concentric thickening rings and splitting (fig. 3, C) so as to detach the wind-dispersed sporangium; 2- or 4-ciliate zoosp. are formed on subsequent moistening; (*b*) sessile sporangia (fig. 80, B–E), which are terminal, lateral, intercalary, or rarely axillary and are formed merely by enlargement of a cell without thickening of the septum; they do not become detached and always produce 2-ciliate swarmers which in some cases at least behave as isogametes[2]; (*c*) Brand's "funnel-sporangia" formed from the apical part of a terminal cell, the septum lying between two superposed thickening rings and the outer layer of the original cell-wall splitting at the level of the septum, these sporangia likewise becoming detached at maturity. The sporangia open by a terminal or subterminal pore.

Sp. of *Trentepohlia* are most abundant in damp tropical or sub-tropical climates, occurring profusely as epiphytes on the leaves and

[1] Wille, 1887, p. 426; Meyer, Bot. Zeit. LXVII, 1909, p. 25; Brand, Beihefte Bot. Centralbl. XII, 1902, p. 200; Brand, Ber. Deutsch. Bot. Ges. XXVIII, 1910, p. 83; Senn, Verh. Schweiz. Naturf. Ges. Solothurn, XCIV, 1911; West and Hood, New Phytol. X, 1911, p. 241; Geitler, Österr. Bot. Zeitschr., 1923, p. 76.

[2] The underlying cell often grows subsequently into the empty sporangium either forming a new sporangium or a branch.

bark of trees; they are also found commonly in mountainous regions, which is indeed their chief habitat in the Brit. Isles. They form the algal component of a number of Lichens (e.g. *Graphis*). Only four sp. are certainly recorded from Great Britain. Of these the most abundant is *T. aurea* Mart. which occurs principally in mountainous districts,

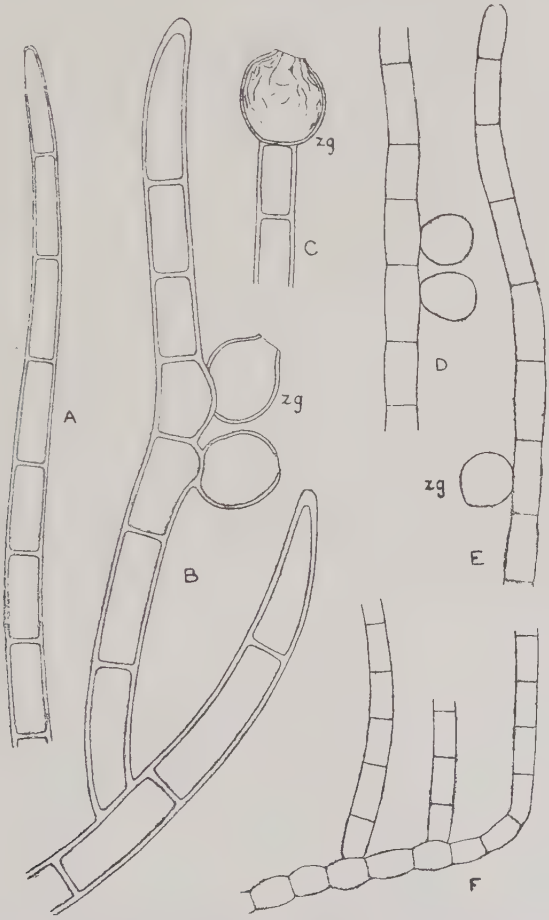

Fig. 80. A–C, *Trentepohlia aurea* (L.) Mart. var. *lanosa* Kütz., from Cookridge, W. Yorks (× 500). D–F, *T. calamicola* (Zell.) De Toni, from trees near Lough Gartan, Donegal, Ireland (× 500). *zg*, sporangium.

chiefly attached to the windward side of rocks, particularly Carboniferous limestone or Silurian rocks. It forms broad expanded sheets of a bright red or orange-red colour; filaments 10–20 br. (cf. fig. 80, A–C). *T. umbrina* (Kütz.) Bornet, in which the projecting system is

little developed and which is found on tree-trunks and wood-work, and *T. calamicola* (Zeller) De Toni et Levi (filaments 7·5–10 br.) (fig. 80, D F) are considerably rarer. *T. odorata* (Ag.) Wittr., which West (1904, p. 95) regarded as synonymous with *T. umbrina*, is likewise rare.

Phycopeltis Millardet, 1870[1] (*Hansgirgia* De Toni, 1889) is as yet unrecorded for the Brit. Isles, but *P. epiphyton* Millard. (fig. 79, B) is not an uncommon epiphyte on leaves of *Abies*, *Hedera*, *Rubus*, etc. on the continent, forming greenish or orange-yellow specks due to a compact 1-layered disc-like stratum. Reprod. is effected by 2-ciliate ovoid zoosp., formed in stalked detachable sporangia terminal on short upright filaments, and by smaller 2-ciliate gametes produced from the central cells of the disc.

Family 3. COLEOCHAETACEAE

This includes the single genus

Coleochaete de Brébisson, 1844[2]. Thallus aquat., epiphytic, often enveloped in mucilage, appearing either as hemispherical cushions composed of prostrate and projecting threads with apical growth, or more commonly as 1-layered discs without projecting threads and showing marginal growth; the discs consist of branched filaments which radiate from a central point and either form a compact layer or are partly not in lateral contact. Cells uninucleate, with a single parietal chloropl. of irregular shape having one or two large pyrens. Many of the cells bear characteristic sheathed setae originating as a protrusion of the wall; the outer layers soon rupture and form the basal sheath, whilst the inner layers lengthen to produce the actual seta which contains a slender thread of cytoplasm (cf. figs. 68, A; 81).

Asex. reprod. is effected in spring and early summer by large ovoid 2-ciliate zoosp. (fig. 68, D) formed singly from the contents of the ordinary cells and escaping through a round orifice. In germination the zoosp. divides either horizontally into two cells of which the upper forms a hair whilst the lower divides in two directions to form the disc (*C. scutata*), or vertically into two cells which constitute the centre from which the creeping threads develop.

The sexual reprod. takes place from May to July and shows an advanced type of oogamy. In *C. pulvinata* the oogonia appear as flask-shaped structures provided with a long neck (trichogyne) containing only colourless cytoplasm; they are borne terminally on short side branches of the projecting

[1] Millardet, Mem. Soc. sc. nat. Strasbourg, VI, 1870, p. 42.

[2] Pringsheim, Jahrb. Wiss. Bot. II, 1860, p. 1; Jost, Ber. Deutsch. Bot. Ges. XIII, 1895, p. 433; Oltmanns, Flora, LXXXV, 1898, p. 1; Chodat, Bull. Herb. Boissier, VI, 1898, p. 457.

system, but are later often pushed into a lateral position by the development of a branch from the underlying cell. In the discoid forms, where they appear as bulging hemispherical structures with the neck represented at best by a papilla, their position is similarly terminal. Here they originate by enlargement of occasional marginal cells, those not involved continuing the peripheral growth of the disc. The oogonia therefore later appear intramarginal and, since two or more series may develop consecutively, they occur in rough concentric zones.

The antheridia of *C. pulvinata* are borne in clusters at the ends of projecting branches (fig. 68, A, *a*) from which they are cut off as small colourless cells, and they occupy an analogous position at the margin of the disc in most of the discoid species. In

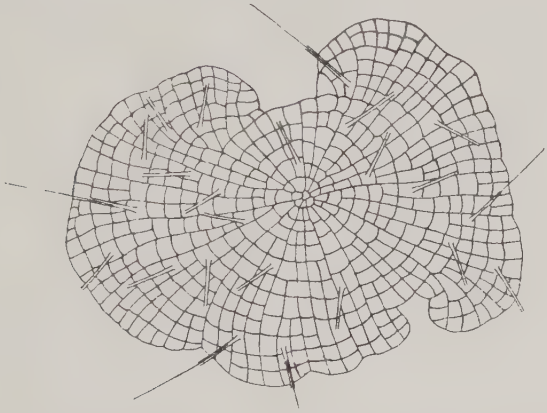

Fig. 81. *Coleochaete scutata* Bréb. (×100), from Welsh Harp, Middlesex.

C. scutata, however, they originate by repeated division of any cell and here alone the resulting spermatozoids are green; in all other cases they are colourless. Each antheridium produces only one 2-ciliate spermatozoid which is liberated by rupture of the apex and gains access to the ovum by gelatinisation of the tip of the neck or papilla.

After fertilisation the oospore becomes surrounded by a wall and enlarges considerably. At the same time the oogonium becomes overgrown by threads originating from the adjacent cells and ultimately forming a complete pseudoparenchymatous investment (fig. 68, A, *o*); in the discoid types this envelope is formed only on the side away from the substratum. A thick brown membrane then develops around the oospore and, according to Oltmanns, this is formed partly from the oogonial

wall and partly from the inner membranes of the investing cells. After the winter period of rest the contents of the oospore divide into two by a wall at right angles to the long axis of the original oogonium and each half divides further into 8 or 16 cells; the envelope is then burst (fig. 68, B) and each cell gives rise to a zoospore (fig. 68, C) differing considerably from that formed by the ordinary thalli. It would seem that in some cases these zoospores only produce dwarfed thalli[1] which are purely asexual, but it is uncertain how far this is the rule. Allen showed that reduction takes place at the first division of the oospore.

The sp. of *Coleochaete* occur attached to the submerged organs of various aquat. and marsh plants, sometimes appearing to the naked eye as tiny green specks. Six sp. are recorded for the Brit. Isles. The most abundant are *C. scutata* Bréb. (fig. 81) and *C. soluta* Pringsh. The former possesses a compact discoid thallus, whilst in the latter there are distinct dichotomously branched filaments radiating in one plane from one or more central cells. In either case the diam. of the disc scarcely exceeds 700–800 μ, the cells averaging 10–23 μ in breadth. *C. orbicularis* Pringsh. forms a circular disc, reaching a diameter of 4 mm., in which the filaments are very closely packed and the cells rather small (8–12 br.). *C. irregularis* Pringsh. has a more or less parenchymatous thallus in which the branching is very irregular. *C. Nitellarum* Jost is endophytic in the cell-membranes of Characeae and has very thin cell-walls. *C. pulvinata* A. Br. (fig. 68) forms hemispherical cushions, commonly 2–4 mm. in diam., but occasionally greatly exceeding these dimensions; it differs from all the preceding in the abundant formation of projecting threads, the cells being 20–25 br. and 1–3 times as long. This sp. is more frequently observed with sexual organs than any of the others. All the sp. are readily eaten by pond-snails of the genera *Limnaea* and *Planorbis*.

Family 4. CHAETOPELTIDACEAE

The Algae comprised in this family are probably not closely related to one another, but until their affinities are more clearly established it is convenient to class them together. They are all reduced aquatic forms, the only common characteristic lying in the development of one or more setae from the membranes of the cells; in some genera the setae have a basal sheath. The majority of the forms here included are epiphytes and, although a few are free-floating, none are planktonic; several are reduced to a practically unicellular condition. There is usually a single parietal chloroplast. Reproduction by zoospores has been observed in several cases; no special sporangia are differentiated.

[1] cf. Lambert, Tufts College Studies, III, 1910, p. 61.

Sub-family 1. CHAETOPELTIDEAE

Setae unbranched, without a basal sheath.

Chaetopeltis Berthold, 1878[1] (incl. *Myxochaete* Bohlin, 1894). Thallus epiphytic, a flat almost circular plate, usually of a single layer of cells more or less radiating from the centre, enveloped by mucilage and with marginal growth; from the upper surface

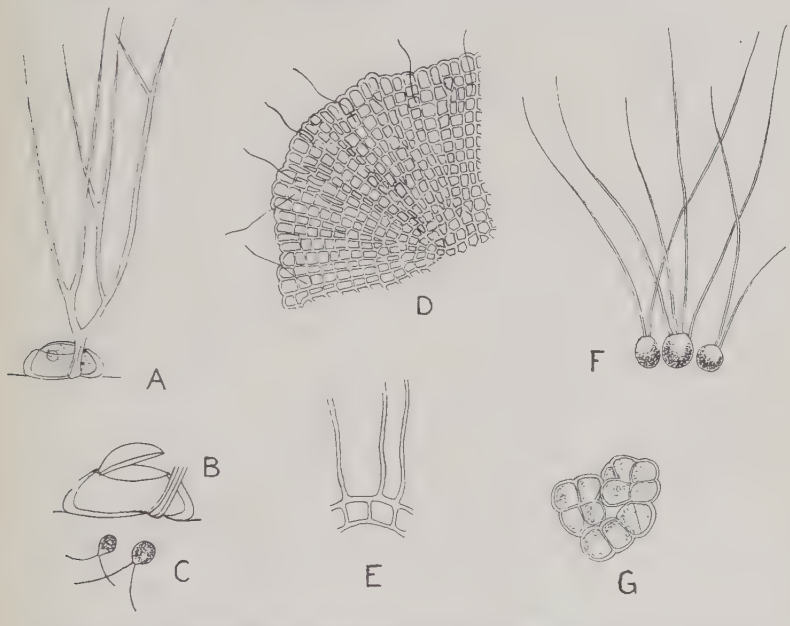

Fig. 82. A–C, *Dicranochaete reniformis* Hieron., from Harborne, Birmingham (after Hodgetts, A and C ×360, B ×600); B, cell which has dehisced to allow of the escape of zoospores; C, zoospores. D–E, *Chaetopeltis orbicularis* Berthold (after Berthold); D, part of a large thallus (×175); E, a few cells in section (×325). F, *Oligochaetophora simplex* G. S. West (after West, ×240), from Lough Gartan, Donegal, Ireland. G, *Pleurococcus Naegelii* Chod. (after Chodat, ×480).

arise a number of scattered mucous setae which are simple and of considerable length, but they may be absent. Cells with thick gelatinous walls and a single parietal, often much lobed and perforated, chloropl. with a single pyren. Reprod. by 4-ciliate ovoid zoosp., 2–8 of which arise from a cell, and by 2-ciliate isogametes.

[1] Berthold, 1878, p. 215; Moebius, Ber. Deutsch. Bot. Ges. VI, 1888, p. 242; Huber, 1892, p. 297; Borzi, Stud. Algologici, II, 1895, p. 329.

C. orbicularis Berthold (fig. 82, D, E) is not uncommon in this country as an epiphyte on stems and leaves of aquatic Phanerogams; the thallus varies greatly in size, sometimes reaching 1 mm. in diameter.

Polychaetophora W. & G. S. West, 1903[1]. Free-floating, unicell. or more usually composed of short, loosely connected filaments of six or eight cells. Cells subglobose, ellipsoid, or ovoid, with exceedingly thick and lamellose walls bearing 8–12 long delicate flexuose setae attenuated to fine points and radiating in every direction; walls sometimes with a large stratified

Fig. 83. *Polychaetophora lamellosa* W. & G. S. West, from Cirencester, Gloucestershire (×370).

outgrowth on one side. Chloropl. single, bright green, sometimes distinctly parietal, but frequently subcentral and filled with oil-globules; pyrens. doubtful. Multiplication by div. of the cells in two directions.

P. lamellosa W. & G. S. West (fig. 83), the only sp., has been found in Gloucestershire among *Tolypothrix pygmaea*: cells 19–35 br.; walls 2·8–10·5 thick; setae 86–183 long.

Oligochaetophora G. S. West, 1911[2]. Epiphytic, the subglobose or ovoid cells loosely aggregated to form very small colonies with but a slight attachment to the substratum. Cell-wall very thin and homogeneous, bearing on the dorsal surface of the cell 2–4 long flexuose setae. Chloropl. single, parietal, cup-shaped, with two or three small starch-granules. Reprod. unknown.

[1] West and West, 1903, p. 79; West, 1911, p. 88.
[2] West, 1908, p. 279; West, 1911, p. 89.

O. simplex G. S. West (=*Polychaetophora simplex* G. S. West) (fig. 82, F) is known from Lough Gartan, Donegal; cells 15–20 br.; setae 50–210 long. It may be doubted whether it is generically distinct from *Polychaetophora*.

Sub-family 2. Dicranochaeteae

Setae devoid of a basal sheath, repeatedly forked.

Dicranochaete Hieronymus, 1887[1]. Cells epiphytic, kidney-shaped or globose, rarely united into short rows, bearing a single forked seta (rarely several) of hyaline gelatinous pectic substance, sometimes of considerable length. Chloropl. like an inverted watch-glass, with or without a pyren.; cells uninucleate. Reprod. by 2-ciliate zoosp. (4–32 per cell) liberated by the detachment of a lid (fig. 82, B, C); the swarmers may occasionally behave as gametes and produce a 4-ciliate zygote which like the zoosp. soon comes to rest. Resting spores formed from the contracted cell-contents and enveloped by a thick membrane also known.

The two sp., though rare, are both found in this country. *D. reniformis* Hieron. (fig. 82, A), with kidney-shaped cells (10–35 br.; 6–13 high) and the seta arising from the ventral notch, is known from various parts of the country having been first recorded by Hodgetts (loc. cit.); his specimens (var. *laevis* Hodgetts) lack the cone-shaped tubercles on the convex wall of the continental form. *D. britannica* G. S. West has more or less globose cells (18–36 br.) with a thick lamellose wall and dorsally attached setae, and is probably epiphytic on *Sphagnum*.

Sub-family 3. Chaetosphaeridieae

Setae provided with a basal sheath.

Chaetosphaeridium Klebahn, 1892[2]. Epiphytic on larger Algae and other aquatics, generally as loose aggregates of small spherical cells, sometimes enveloped in mucilage and occasionally forming short creeping filaments; in the latter case the cells are sometimes connected by short empty cylindrical tubes (utricles). Each cell bears on its free surface an often very long and delicate seta surrounded by a basal sheath which appears as a small conical projection from whose apex the seta emerges; the setae are fragile and commonly break off. Chloropl. parietal, plate-shaped, with one pyren. Div. of the cells sometimes takes place by a horizontal wall, the lower daughter-cell migrating to one

[1] Hieronymus, Cohn's Beitr. z. Biol. d. Pfl. v, 1890, p. 351; West, 1912, p. 329; Hodgetts, New Phytol. xv, 1916, p. 108; Grove, 1920, p. 31.

[2] Klebahn, Jahrb. Wiss. Bot. xxiv, 1892, p. 268; Hazen, 1902, p. 228.

side or developing a tubular outgrowth into which the protoplasm passes, the apical part becoming cut off from the empty part (the utricle) behind. Reprod. by zoosp., four of which are formed in a cell.

C. globosum (Nordst.) Klebahn (*Aphanochaete globosa* Nordst.[2]) is widely distributed in the Brit. Isles, occurring chiefly in the *Sphagnum*-pools of permanent bogs. The cells are 11–18 br., loosely associated, and occasionally surrounded by a gelatinous envelope (fig. 84, A and B). In var. *depressum* the cells are much depressed (fig. 84, C). *C. Pringsheimii* Klebahn (=? *Aphanochaete globosa* var. *minor* Hansg.) is known from N. Yorks (West and West, 1901, p. 22); the cells are 9–11 br., there is no mucilage-envelope, and utricles are generally well developed. Possibly the two sp. are merely forms of one.

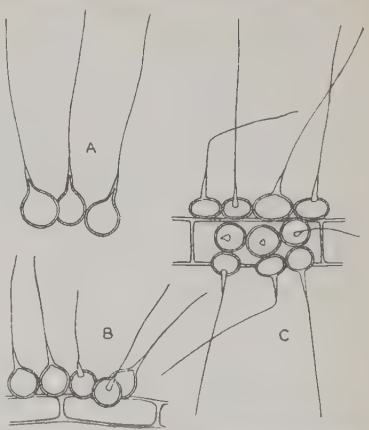

Fig. 84. A and B, *Chaetosphaeridium globosum*[1] (Nordst.) Klebahn: A, from Esher Common, Surrey; B, from Bowness, Westmorland. C, *C. globosum* var. *depressum* (W. & G. S. West), from the New Forest, Hants. (All ×370.)

Conochaete Klebahn, 1893[3]. Epiphytic, composed of loosely

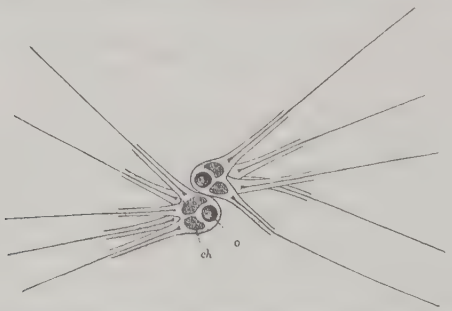

Fig. 85. A, form of *Conochaete comosa* Klebahn, from the New Forest, Hants (×370). *ch*, chloroplast; *o*, oil-globule.

[1] G. S. West (1916 *a*, p. 208, fig. 136) subsequently described these figures as *C. Pringsheimii* Klebahn; this sp. however, except in its f. *conferta*, usually shows well-marked utricles and the cells are smaller than those of *C. globosum*, which would appear to be the common British species.

[2] Borzi (Nuov. Notarisia, III, 1892, p. 50) founded a genus *Nordstedtia* based on *Aphanochaete globosa* Nordst. Klebahn, who compared Nordstedt's original specimens with Borzi's drawings of *Nordstedtia*, however, states that the latter represents an entirely different plant.

[3] Klebahn, Jahrb. Wiss. Bot. XXV, 1893, p. 310; West and West, 1903, p. 79.

aggregated cells embedded in mucilage. Cells subglobose, markedly dorsiventral, often depressed, each with a number of long delicate setae radiating in all directions; setae arising from the apex of a mammillate protuberance of the cell-wall or from the base of an elongated sheath. Chloropl. one or two per cell, each with one pyren.; a prominent oil-globule often in the basal half of the cell. Reprod. by div. in two directions and by zoosp., four or eight formed from each cell.

The two Brit. sp. are both exceedingly rare. *C. comosa* Klebahn (fig. 85) has cells 13–26 br. bearing 3–5 setae sheathed at the base. In *C. polytricha* (Nordst.) Kleb. the cells are 10–16 br. and the setae arise from the apices of mammillate protuberances of the stratified wall.

Family 5. PLEUROCOCCACEAE

This includes only the genus

Pleurococcus Meneghini, 1842; emend. Naegeli, 1849[1] (*Protococcus* Agardh. 1824. in part). Terrestrial (and aquat.??), unicell., cells when mature isolated and more or less globose, but frequently in groups of two, three, four, or more owing to slow rounding off of the products of div. In moist places short filaments showing simple branching are often produced as a result of div. mainly in one direction; these filaments readily arise in cultures. Cell-walls strong and firm; protoplast without visible vacuoles, containing one parietal more or less lobed, often massive chloropl.; a pyren. does not usually appear to be present, but there may be rare forms in which it occurs. Reprod. by vegetative div. in three directions followed by subsequent separation of the cells; 2-ciliate zoosp. and isogametes recorded, but highly doubtful.

There is probably no other Alga about which there has been so much confusion as about the genus *Pleurococcus*. Many of the sp. that have been ascribed to it belong to *Chlorococcum*, *Chlorosphaera*, *Trebouxia* (*Cystococcus*), or *Chlorella*, or even to other algal classes, and until relatively recent times many algologists have tended to describe as a sp. of *Pleurococcus* any globose unicellular form that could not be placed elsewhere, often without any evidence as to its detailed cell-structure or mode of reproduction. There is little evidence that unicellular forms, endowed with the capacity of limitless vegetative division, occur in other than terrestrial situations, and one may hazard

[1] Naegeli, 1849, p. 64; Chodat, 1913, p. 234; Wille, Nyt Mag. f. Naturvidenskab. LI, 1913, p. 7; Pascher, 1915, p. 223; West, 1916, p. 1; Chodat, C. R. Soc. Phys. et d'Hist. nat. Genève, XLI, 1924, p. 105; Brand, 1925, pp. 323, 335.

a conjecture that all the aquatic "species" of *Pleurococcus* belong to other genera. Further, it is probable that the records of zoospores and gametes in the true terrestrial sp. of the genus are due to confusion with *Chlorococcum* and *Trebouxia* which often grow intermingled with *Pleurococcus*, although there is no *prima facie* reason why the latter should lack them. The cells of *Pleurococcus* can withstand desiccation without change (Fritsch, 1922, p. 10) and there is no evidence of the occurrence of special resting-stages.

It is still debatable whether there is more than one species of

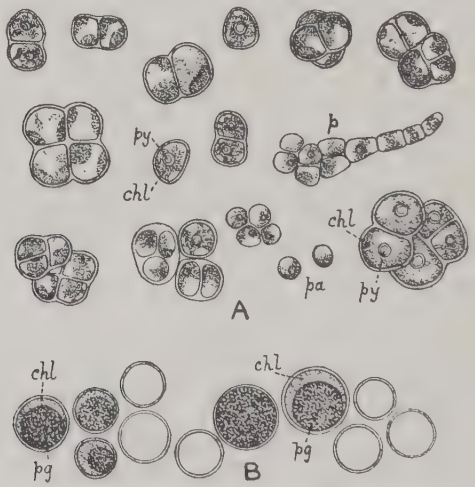

Fig. 86. A, *Pleurococcus Naegelii* Chod., from Cirencester, Gloucestershire; all the cells with a stellate chloroplast and pyrenoid do not belong here, but are forms of *Trebouxia*; *p* and the lowest group on the right-hand side may belong to another species of *Pleurococcus* possessed of pyrenoids. B, *P.* (*Chlorococcum*?) *rufescens* (Kütz.) Bréb. var *sanguineus* W. & G. S. West, from near Arncliffe, W. Yorks. (All ×520.) *chl*, chloroplast; *pg*, bright red pigment; *py*, pyrenoid.

Pleurococcus of frequent occurrence in terrestrial situations. The common form has a somewhat lobed parietal chloroplast without a pyrenoid; there would, however, seem to be another similar Alga in which a pyrenoid is present. Possibly the two are but different races of the same species. The present writer is of the opinion that the majority of the stages figured by Chodat (1902, figs. 191–194) as *P. vulgaris* Menegh., as well as certain cells shown in fig. 86, A, belong to *Trebouxia* (*Cystococcus*), with which there has certainly been much confusion in the past.

Wille (loc. cit.), having examined the original specimens of *Protococcus viridis* Ag. in Agardh's herbarium, found them to

be identical with *Pleurococcus Naegelii* Chod. (*P. vulgaris* Naeg.). Wille, G. S. West, Chodat, and others have thereupon advocated readopting the name *Protococcus* for this common terrestrial genus, but to this there are prominent objections (cf. also Brand, 1925, p. 324). The name *Pleurococcus*, however much misused, is quite definitely associated in the minds of all botanists with the green powder-like growth covering tree-trunks and the like, whereas *Protococcus* is a synonym for the most diverse genera of green Algae, including Chlorococcales, Volvocales, etc.; in the words of G. S. West (1904, p. 230): "The latter genus is obsolete, having included Algae which are now referred to a number of other genera." To resuscitate *Protococcus* would no doubt lead to further confusion, where confusion is already rampant.

In a very valuable study of the unicellular aerophilous members of Isokontae as they occur in nature, Brand (1925, p. 336) regards as the type of the genus *Pleurococcus* the species *P. vulgaris* of Meneghini[1]. This was based on *Chlorococcum vulgare* of Greville[2], but a perusal of the latter's figures shows very few points of resemblance, except for the occurrence in both forms of vegetative division. This last characteristic (with the resulting tendency of the cells to cohere in packets) was probably the principal feature in Meneghini's concept of the genus *Pleurococcus*. The figures he gives of *P. vulgaris* are however evidently those of a *Prasiola*-like form, and Brand's careful study of what is clearly the same Alga altogether confirms this view (cf. also loc. cit., p. 337). It may be doubted whether this form is generically distinct from *Prasiola*, if it be not a stage in the development of a species of the latter. There is no evidence that it has so far been found in this country, and Brand speaks of it as rare.

There does not appear, however, to be any valid reason for accepting this particular form as the type of *Pleurococcus* to the exclusion of all others. Greville's figures of *Chlorococcum vulgare* seem to indicate a parietal rather than an axile chloroplast (cf. his fig. 4), and in any case accord much better with the *Pleurococcus vulgaris* of Naegeli[3] than with that of Meneghini. It would seem best therefore to transfer the *P. vulgaris* of Meneghini to Prasiolaceae and, if its independence be proved, to establish a new genus for it, whilst *Pleurococcus* remains for the Algae characterised by a parietal chloroplast and vegetative division. The commonly occurring form of this genus may well retain, to avoid confusion, the name *P. Naegelii* which Chodat has given to it. Brand (1925, p. 344) has given a careful description of this

[1] Monogr. Nostoch. Ital., 1842, p. 38, tab. V, fig. 1.
[2] Scott. Crypt. Flora, Edinburgh, v, 1827, p. 262.
[3] Naegeli, 1849, p. 65, tab. IV, E, fig. 2.

species under the name *Desmococcus vulgaris*, but for the reasons just mentioned a new name is regarded as unnecessary.

In placing *Pleurococcus* amongst Chaetophorales the writer is following the practice advocated by Chodat[1] and Oltmanns (1922, p. 304) which is no doubt a sound one. In cell-structure it perhaps stands nearer to Chaetophoraceae than to Trentepohliaceae, but Pascher's *Iwanoffia* (cf. p. 175) shows that the Chaetophoraceae also have terrestrial representatives. It may be doubted whether *Pleurastrum insigne* Chod. (*Pseudopleurococcus vulgare* Snow)[2] is more than a stage of *Pleurococcus*.

P. Naegelii Chod. (*P. vulgaris* Naeg. non Meneghini; *Protococcus viridis* Ag.; *Chlorococcum vulgare* Greville; *Desmococcus vulgaris* (Naeg.) Brand) is one of the commonest Algae, occurring in great profusion in all kinds of damp situations, usually as a thin green incrustation on the windward side of stones, walls, palings, tree-trunks, etc. The chloroplast is a massive lobed plate without (or sometimes with?) a pyrenoid; cells 9–20 br. (figs. 82, G; 86, A, in part). Another possible sp. is *P. dissectus* (Kütz.) Naeg.

P. rufescens (Kütz.) Bréb. is probably a sp. of *Chlorococcum*: the cell-contents have a brick-red colour owing to the presence of haematochrome which usually appears dissolved in an oil. This form has a preference for calcareous rocks; the var. *sanguineus* W. & G. S. West has been observed in the limestone districts of W. Yorks. forming large brilliant blood-red patches on those stones and rocks in the beds of streams which could not be displaced by the current and are often left dry; cells 11–20 br.

According to Paulson[3] *Pleurococcus* is the algal constituent of certain sp. of the Lichen *Dermatocarpon*.

GROUP 5. OEDOGONIALES

The Oedogoniales are a sharply circumscribed group affording but few points of affinity with other Isokontae. Whatever the ancestry, no intermediate forms have lasted to the present day. Like the Conjugatae they are an essentially freshwater group, playing a very important rôle nearly all the world over in the algal vegetation of smaller pieces of water; the peculiar *Oedocladium*[4] is however terrestrial. The remaining genera, *Oedogonium* and *Bulbochaete*, together include more well-established species[5] than any two other genera of filamentous Green Algae;

[1] Bull. Herb. Boissier, II, 1894, p. 616.

[2] Snow, Ann. of Bot. XIII, 1899, p. 189; Chodat, Bull. Herb. Boissier, VII, 1899, p. 827.

[3] Trans. Brit. Mycol. Soc. VII, 1921, p. 46.

[4] Not yet recorded in the British Isles.

[5] An excellent monograph of the group has been compiled by Hirn (Act. Soc. scient. Fennicae, XXVII, 1900 and XXXIV, 1906).

since however specific distinction is almost entirely based on the characters of the sexual organs, determination of sterile material is usually impossible.

Oedogonium consists of long unbranched threads, generally free-floating in the mature condition, but attached by a specially modified basal cell (fig. 87, B) when young; in species inhabiting

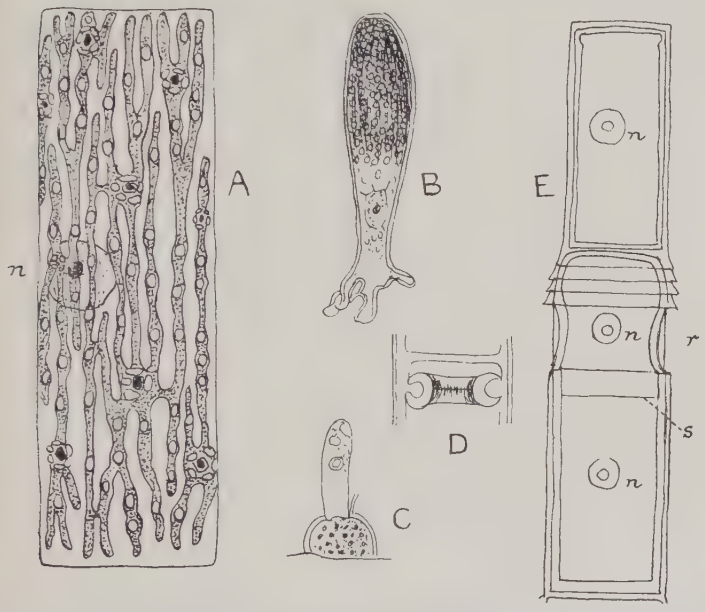

Fig. 87. A, single cell of *Oedogonium* sp. showing the large nucleus *n*, and the reticulate chloroplast (after Schmitz, ×700). B, *O. concatenatum* Wittr. (after Hirn, ×300) and C, *O. rufescens* Wittr. (after Scherffel, ×400), germinating zoospores. D, upper end of an *Oedogonium*-cell (after Strasburger) showing the ring of thickening. E, two cells of *Oedogonium*, the lower in process of division (after van Wisselingh, ×435). *n*, nucleus; *r*, thickening ring; *s*, septum.

flowing water the basal attachment naturally persists. *Bulbochaete*, on the other hand, is richly branched (fig. 92), the branches being unilateral, and each cell bears a long colourless hair with a bulbous base; the terminal cells have two such hairs. *Bulbochaete* is smaller than *Oedogonium* and generally attached. In *Oedocladium*[1], which inhabits damp mud, there is a branched creeping filament sending colourless rhizoids into the

[1] Stahl, Jahrb. Wiss. Bot. XXIII, 1891, p. 339; Collins, Tufts Coll. Stud. IV, No. 7, 1918. p. 71.

substratum and bearing erect green branched threads on its upper side. The cells in all cases contain a single, often large nucleus and an elaborate reticulate cylindrical chloroplast with narrow subparallel meshes[1] and numerous scattered pyrenoids (fig. 87, A); the cell-wall is usually not conspicuously thickened and but scanty formation of mucilage occurs.

One of the outstanding characteristics of the Oedogoniales lies in the peculiar method of growth of the cell-wall. Some time prior to division of a cell of *Oedogonium*[2] a transverse ring of thickening appears at the upper end, just beneath the septum (fig. 87, D); in optical section the fully developed ring is seen to consist of a central (mucilaginous?) portion and a firmer bounding layer of cellulose adjoining the protoplast and intimately concrescent with the inner layer of the old membrane above and below the ring. Nuclear division is followed by the formation, across the middle of the cell, of a septum which however for some time remains unconnected with the longitudinal walls. Soon after, the cell-membrane breaks across transversely at the level of the ring and the latter gradually becomes stretched to form a new cylindrical piece (fig. 87, E), intercalated between the parts (cap and sheath) of the old wall; simultaneously the septum becomes displaced upwards, till it takes up a permanent position near the edge of the lower part of the ruptured wall. The upper of the two daughter-cells has a wall formed mainly from the stretched thickening ring, but at its top end there is a slightly projecting "cap" constituted by the small part of the original membrane left above the point of rupture; the lower cell is almost entirely encased in the "sheath" formed by the lower part of the old cell-membrane. "Cap-cells" usually divide repeatedly, exhibiting as many caps as there have been divisions, and the presence of such cells is a safe criterion for the recognition of a species of *Oedogonium*. In most cases (cf. however p. 220) the young plant derived from a zoospore divides after this manner from the first.

In *Oedogonium* growth is intercalary, cap-cells arising at variable intervals in the course of the threads, but in many species of *Bulbochaete* it is strictly basal and not more than one

[1] According to unpublished observations of Dr Nellie Carter on an undetermined species of *Oedogonium*, the chloroplast may here consist either of a greatly attenuated network or, at the other extreme, of an almost entire cylinder. There may also be prolongations invading the cell-cavity, as in *Cladophora*.

[2] Hirn, loc. cit., 1900, p. 5, and 1906, p. 2; Fritsch, Ann. of Bot. XVIII. 1904, p. 652; Kraskovits, Sitz.-ber. K. Akad. Wiss., Wien, Mat.-Nat. Kl., CXIV, 1905, p. 237; v. Wisselingh, Beihefte Bot. Centralbl. XXIII, 1908, Abt. 1, p. 157.

cap is usually formed on a cell[1]. In the unicellular plant developed from the zoospore a small colourless hemispherical cell is cut off apically by an ordinary septum; the external wall of this cell is ruptured (being turned to one side like a lid) and its contents, secreting a new membrane, grow out as the first hair. The cell below develops a thickening ring at its upper end and divides as above described for *Oedogonium*; the lower cell sooner or later again divides and thus a multicellular main axis originates in which the oldest cell is at the top and the youngest next to the basal cell. Each cell, after its formation, grows out slightly at its apex towards one side or the other, and this protrusion is cut off as a colourless cell; its contents lengthen into

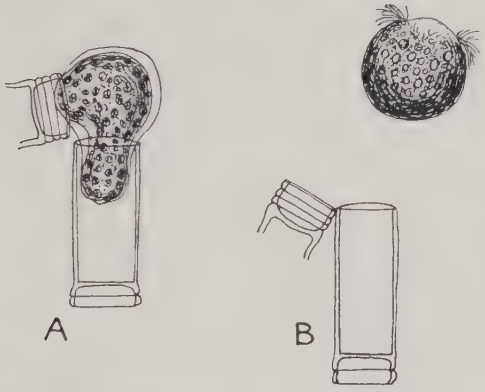

Fig. 88. A and B respectively show two stages in the escape of the zoospore of *Oedogonium concatenatum* Wittr. (after Hirn, ×260).

a hair as above described, the ruptured wall forming an irregular sheath around the base (not shown in fig. 92). The terminal cell therefore bears two, the other cells one hair each. Each cell of a *Bulbochaete* thus has a plane base, whilst the upper end is composed of two faces forming an obtuse angle with one another, the one bearing a hair, the other the next cell of the thread (cf. fig. 92). At more or less numerous points rings of thickening are formed below the septa which cut off the hairs; the ensuing division leads to the cutting off of a lateral cell, the first one of a branch which likewise exhibits basal growth. In *Oedocladium* growth is apical, but there is a tendency for the caps to drop off after some time.

[1] Pringsheim, Jahrb. Wiss. Bot. 1, 1858, p. 20; Hirn, loc. cit., 1900, p. 10. In some species with elliptical oospores, however, intercalary growth occurs as well.

The peculiar method of cell-enlargement thus found in all Oedogoniales finds a slight parallel in the early growth of the young plants of some species of *Microspora* (cf. p. 164), but there are marked differences.

Apart from the usual fragmentation, prolific reproduction takes place by means of large multiciliate zoospores, always produced singly from the ordinary cells[1]. Their development takes place rapidly and the stages are readily followed. A slight contraction of the protoplast is succeeded by the appearance towards one side of a colourless patch, around whose base the arising cilia are seen as fine striae. Soon the cell-wall ruptures near one end, the two halves gape apart, and the zoospore slowly glides out (fig. 88, A). At the time of liberation it is momentarily enveloped by a delicate mucilage-vesicle, but this soon vanishes. The zoospores are almost spherical or pyriform and deep green, but there is a well-marked colourless beak around the base of which the usually short[2] cilia arise (fig. 88, B); an eye-spot is often distinguishable. In the majority of cases (cf. however p. 220) it is the anterior end of the zoospore that becomes adpressed to the substratum and that develops into the often richly lobed disc (fig. 87, B) by which attachment is effected[3]. In *Oedocladium* vegetative multiplication by means of short rows of two, three, or more cells (akinetes) filled with food-reserves also occurs.

Sexual reproduction appears to take place readily in many species and is of an advanced oogamous type[4]. Oogonia and antheridia are produced in the same thread in some species of *Oedogonium* (fig. 89) and *Bulbochaete*, but the majority are dioecious; most of these (nannandrous species) exhibit a curious dimorphism of the sexual plants, the oogonia being produced in the ordinary threads, the antheridia in special "dwarf-males" consisting at the most of only a few cells (fig. 91, *n*). These dwarf-males originate from a special type of swarmer, called an androspore, produced singly within flat discoid cells (androsporangia) formed by repeated transverse division of the ordinary cells. These androsporangia occur either in the same filaments as the oogonia (gynandrosporous species) or in distinct filaments (idioandrosporous species). The androspores are smaller than the zoospores and sometimes yellowish in colour, but otherwise

[1] cf. Pringsheim, loc. cit., p. 25; Klebs, 1896, p. 264 et seq.

[2] Hodgetts (New Phytol. XIX, 1920, p. 258) has described zoospores of *Oedogonium cryptoporum* with relatively long cilia.

[3] cf. Wille, 1887, p. 454; Fritsch, Ann. of Bot. XVI, 1902, pp. 412 and 467, and XVIII, 1904, p. 648; Scherffel, Ber. Deutsch. Bot. Ges. XIX, 1901, p. 557.

[4] See especially Pringsheim, loc. cit., p. 29; Juranyi, Jahrb. Wiss. Bot. IX, 1873, p. 1; Klebahn, ibid. XXIV, 1892, p. 235; Hirn, loc. cit., 1900, p. 17.

show the same characteristics. At the end of their brief swarming period they settle down either on an oogonium or on one of the adjacent cells and germinate to produce a minute plant which has a rhizoid-like attachment and very soon proceeds to form

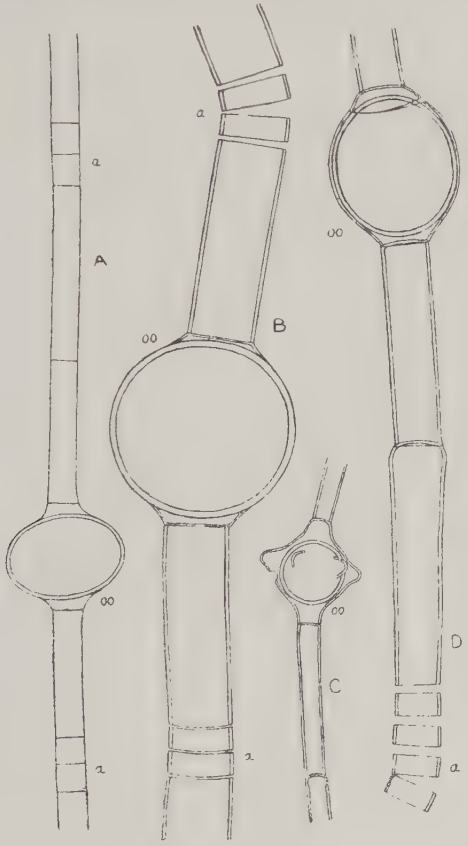

Fig. 89. Monoecious species of *Oedogonium*. A, a form of *O. obsoletum* Wittr., from near Goring, Oxfordshire. B, *O. zig-zag* Cleve var. *robustum* W. & G. S. West, from Harefield, Middlesex. C, *O. Itzigsohnii* De Bary var. *minor* West, from the Orkneys. D, *O. Ahlstrandii* Wittr., from Pilmoor, N. Yorks (×460). *oo*, oogonium; *a*, antheridium.

antheridia; in a few species of *Oedogonium* the dwarf-male remains unicellular (fig. 91, B) producing two spermatozoids from its contents.

The antheridia are flat cells (fig. 89, *a*) resembling the androsporangia and formed in the same way. The number of consecu-

tive antheridia is variable, but to some extent characteristic of species; in the dwarf-males from one to four of them may be formed. In most cases the contents of each antheridium divide to form two spermatozoids which usually lie side by side, though superposed in the antheridia of the dwarf-males; the production of only one spermatozoid is rarer. The sperms resemble miniature

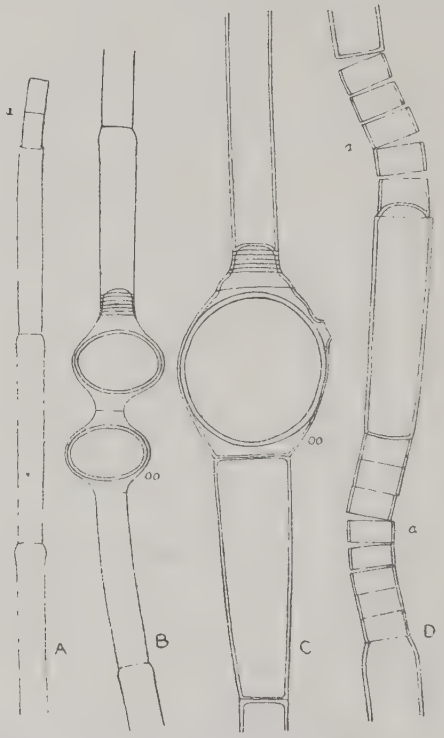

Fig. 90. Dioecious macrandrous species of *Oedogonium*. A, male plant of *O. rufescens* Wittr., from the Scilly Isles. B, female of same. C, female thread of *O. lautumniarum* Wittr., from Welsh Harp, Middlesex. D, male thread of same (×460). *oo*, oogonium; *a*, antheridium.

pale green or yellowish zoospores and are liberated in the same way as the latter.

The oogonia in the vast majority of cases represent prominently enlarged cells (figs. 89, 90). In *Oedogonium* and *Oedocladium* they are formed by a single division of a cap-cell, the upper segment during the stretching of the thickening ring undergoing more or less distention to form the oogonium; the underlying sheath-cell is known as the "supporting-cell" and may in some

species undergo further segmentation to form rows of two, three, or even more oogonia (fig. 91, A). In *Bulbochaete* two divisions are involved in the production of an oogonium, which consequently has two supporting-cells. After the first division the septum becomes fixed at the middle of the sheath (cf. p. 214), so that the membrane of the upper segment is formed by a short cylindrical piece of the latter and above that by the stretching thickening ring which is becoming bulged out to form the oogonium. A second thickening ring then develops in the median region of the young oogonium followed by a transverse rupture of the wall at this point; the septum formed in connection with this second division lies on a level with the top of the first-formed sheath, so that both supporting-cells are included in the latter. This curious development is responsible for the fact that the wall of the mature *Bulbochaete* oogonium can nearly always be seen to consist of three pieces (fig. 92, A).

The contents of the oogonium contract to form a single ovum which, opposite the point of opening, exhibits a well-marked colourless receptive spot (fig. 3, H). In all species of *Bulbochaete*, in *Oedocladium*, and many species of *Oedogonium* the oogonia open by a small pore formed by gelatinisation of the tip of a papilla: its position is of taxonomic importance. In some species of *Oedogonium*, however, opening is effected by a transverse split (operculum) in the wall and a thin membrane deposited on the inner side of the latter forms a definitely shaped conduit, with a more or less circular aperture, leading down to the ovum. In the few cases in which the life-history has been studied a small quantity of slimy protoplasm is extruded from the mature ovum.

The oospores develop a thick, usually three-layered membrane and the contents often assume a red colour; they pass through a prolonged resting period. On germination (only observed in a few cases) the contents are set free still enveloped in a delicate membrane and give rise by division to four ordinary zoospores (fig. 3, I) which lose their red colour during swarming.

Among many peculiarities the most striking feature of the Oedogoniales is no doubt their dwarf-males. In several macrandrous species of *Oedogonium*, however, the male threads are narrower than the female (cf. fig. 90, A and B). There is moreover an occasional tendency for the young plants of *Oedogonium* arising from zoospores to develop antheridia precociously. Such cases may indicate the way in which this habit has arisen[1]. The androspores have, however, also been regarded as prematurely liberated sperm mother-cells[2] and, in the case of *O. diplandrum*

[1] cf. Fritsch, Ann. of Bot. XVI, 1902, p. 478; West, 1912, p. 322.

[2] cf. Juranyi, loc. cit., p. 27; Oltmanns, 1922, p. 340.

where the dwarf-males are unicellular, their division would only be deferred by the intervening swarming period. Pascher[1] regards the macrandrous species as more specialised than the nannandrous ones.

Even if such special characteristics as the dwarf-males and the peculiar growth of the cell-wall be ignored, the Oedogoniales present few points of contact with other filamentous Green Algae. The large zoospores, the elaborate chloroplast, the hairs of *Bulbochaete*, and the complex female organs are almost as peculiar and, although some authorities have compared the Oedogoniales with *Cylindrocapsa*, the resemblances on closer scrutiny appear superficial. The Oedogoniales probably had an origin distinct from that of either Ulotrichales or Chaetophorales, although it is unnecessary to seek it as far back as a separate flagellate ancestry, such as was assumed by those who established the class Stephanokontae for this group.

The three genera are grouped in the single

Family OEDOGONIACEAE

Oedogonium Link, 1820. Filaments simple, unbranched, composed of cylindrical cells, sometimes slightly swollen (capitellate) at their upper ends; terminal cell usually rounded, but sometimes acuminate or drawn out into a long hair. Cell-walls firm; chloropl. with one or many pyrens. Reprod. by fragmentation and by zoosp.: the latter on coming to rest either (*a*) attach themselves by the colourless beak which grows out into a simple or much lobed hapteron (fig. 87, B); or (*b*) flatten out laterally against the substratum to form a "hemispherical" basal cell from the convex surface of which a new thread gradually develops, the membrane of the basal cell at its point of origin becoming detached as a lid[2] (fig. 87, C).

Sex. reprod.: About half the known sp. are nannandrous, and rather more than half the macrandrous forms are monoecious. Oogonia with one supporting cell, spherical or ellipsoidal, rarely of the same width as the veget. cells, usually single, but sometimes in twos or in rows, opening either by a pore or by a split (operculum), whose position in either case is characteristic of the sp.; oospore globose, ellipsoidal, or ovoidal, filling or not filling the oogonium, membrane smooth or more rarely ridged, spiny, punctate, reticulate, etc. Antheridia, cf. p. 217. Dwarf-males rarely unicell., usually with an elongated attaching cell and one or more flat antheridia[3], each producing two superposed

[1] Pascher, Hedwigia, XLVI, 1906, p. 265, esp. p. 275.

[2] cf. Scherffel, loc. cit.

[3] Often interpreted as a uni- or multicellular antheridium.

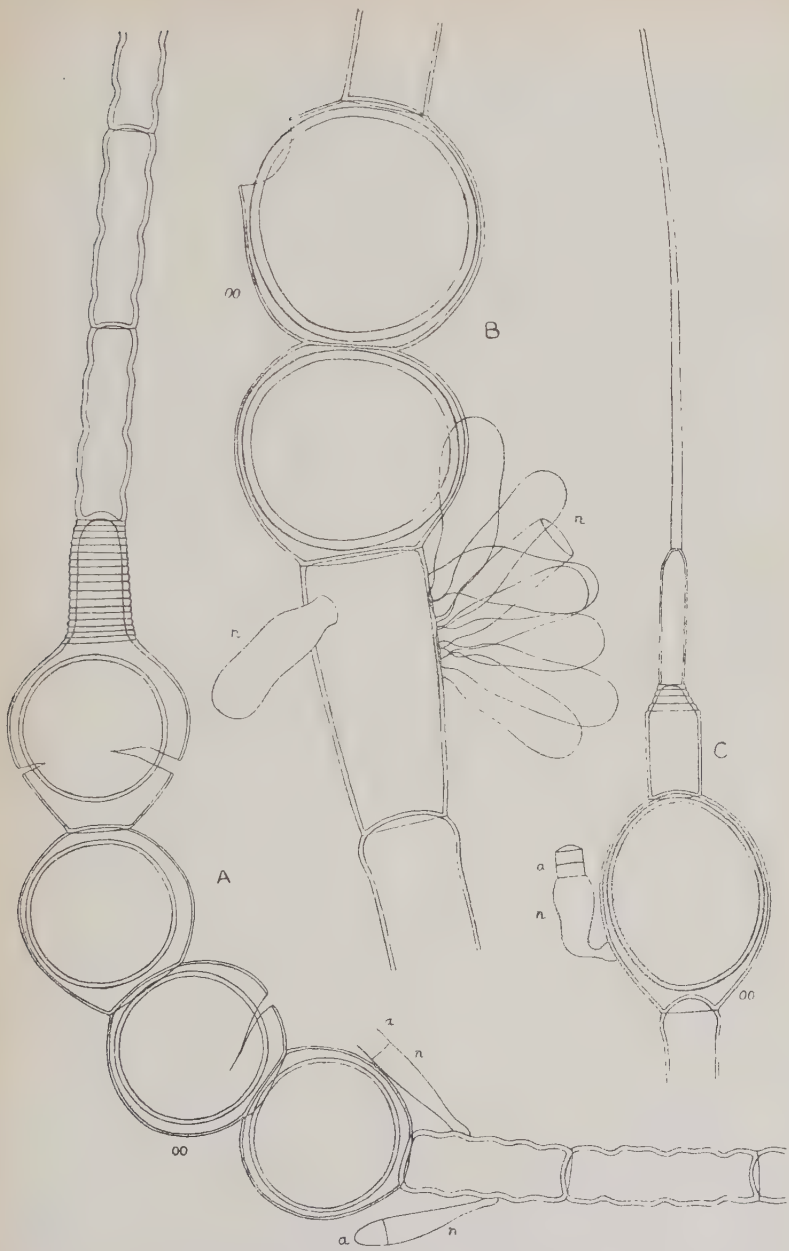

Fig. 91. Dioecious nannandrous species of *Oedogonium*. A, a form of *O. undulatum* (Bréb.) A. Br., from Pilmoor, N. Yorks. B, *O. cyathigerum* Wittr., from Rawcliffe Common, W. Yorks. C, *O. ciliatum* (Hass.) Pringsh., from near Senens, Cornwall (×460). *oo*, oogonium; *n*, dwarf-male; *a*, antheridium.

spermatozoids. The cutting off of the antheridium either takes place by a simple septum ("internal" antheridium, always single) or more commonly with the customary ring-formation, in which case the antheridium is covered by the cap ("external" antheridium). Wille[1] has observed resting spores in some sp.

The adult plants usually occur floating in masses in quiet waters or attached to various aquatics; as the mucous covering on the filaments is very slightly developed they do not feel as slimy as most filamentous Green Algae and afford a substratum for various epiphytes. In the autumn the cells are frequently packed with starch. There are about 80 Brit. sp., exhibiting great variation in dimensions; specific distinction is based on the characters mentioned in the above diagnosis and sterile material, with rare exceptions, is indeterminable. *O. undulatum* (Bréb.) A. Br. (fig. 91, A), however, possesses very characteristic undulate vegetative cells, whilst *O. punctato-striatum* De Bary has the cell-walls furnished with spirally arranged granules. Fructiferous specimens are found especially in small ponds and ditches and more commonly in the S. of England and the S.W. of Ireland than in other parts of Gt Britain. The smallest Brit. sp. is *O. tapeinosporum* Wittr. (2·7–5 br.) and the largest is *O. giganteum* Kütz. (30–50 br.). The general characters of the oogonia and oospores will be gleaned from a study of figs. 89–91. In *O. acrosporum* De Bary there is a single terminal oogonium. Sometimes the supporting cell is much swollen, as in *O. Borisianum* (Le Cl.) Wittr. and *O. lautumniarum* Wittr. (fig. 90, C). Special types are afforded by *O. platygynum* Wittr., where the oogonial wall is plicated, and *O. Itzigsohnii* De Bary (fig. 89, C), where it possesses a transversely disposed ring of conical projections.

The time of maximum abundance of many sp. of this genus has been shown to coincide with the first spells of bright sunshine in the year (cf. Fritsch and Rich, 1913, p. 27; Hodgetts, 1921, p. 34), but that of others is more intimately related to the temperature.

Bulbochaete Agardh, 1817. Filaments branched, usually attached; branches always unilateral on the relative main axis, those of successive axes on alternate sides, each cell bearing to one side or the other a long hair with a swollen base, the terminal cells with two hairs; cells usually widening upwards and generally shorter than in *Oedogonium*. Reprod. as in the latter; *re* germination of zoosp., see p. 215.

Sex. reprod.: Most sp. are nannandrous; the macrandrous ones are monoecious. Oogonia (cf. also p. 219) with two supporting cells, spherical or ellipsoidal, generally terminal on short lateral branches, opening by a more or less superior pore; oospores filling the oogonia, usually with a sculptured membrane. Dwarf-males mostly multicell., with "internal" or "external" (cf. under

[1] Bot. Centralbl. xvi, 1883, p. 217.

Oedogonium) antheridia, commonly situated on the apices of the oogonia.

The sp. prefer very still waters and occur as branched tufts, more often attached than in *Oedogonium*; they possess a quantity of enveloping mucilage, affording a home for numerous Diatoms and often Desmids. The genus is not as abundant as *Oedogonium* and fructiferous

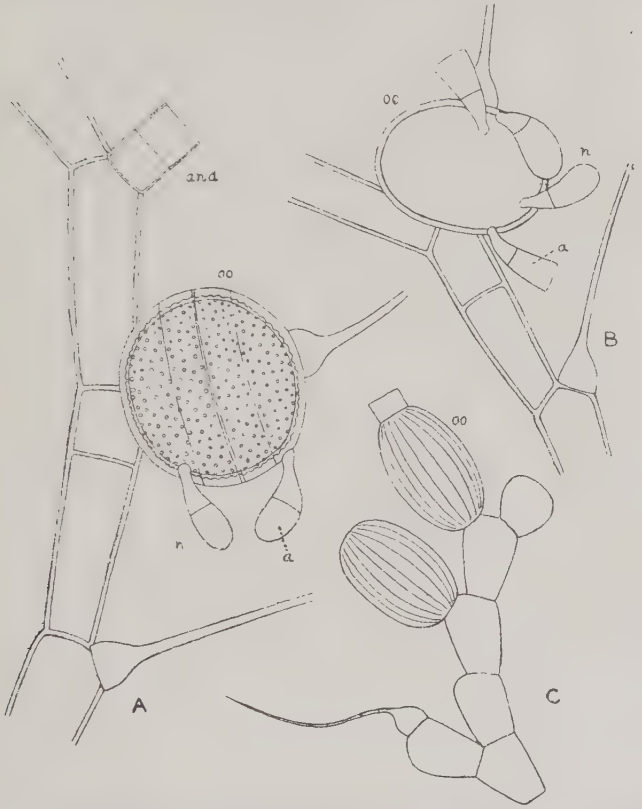

Fig. 92. A, *Bulbochaete subintermedia* Elfv., from near Senens, Cornwall. B, *B. Nordstedtii* Wittr., from near Glendoan, Donegal, Ireland. C, *B. nana* Wittr., from Goring, Oxfordshire (×495). *a*, antheridium; *and*, androsporangium; *n*, dwarf-male; *oo*, oogonium.

specimens are relatively scarce. There are about 14 Brit. sp., of which *B. nana* Wittr. (10–15 br.) (fig. 92, C) is the smallest and *B. gigantea* Pringsh. (24–32 br.) is the largest; the former sp. is macrandrous. In *B. subintermedia* Elfv. (fig. 92, A) and *B. crassiuscula* Nordst. the outer layer of the oospore membrane is scrobiculate, whilst in *B. nana* it is ridged.

GROUP 6. CONJUGATAE

The Conjugatae are a well-defined group and very little experience is necessary to recognise one of its members, characterised as they are by the usual marked symmetry of the cell and an elaboration of the chloroplasts unparalleled in any other group. Apart from these characteristics, which are obvious already in the vegetative phase, the Conjugatae are further distinguished by the complete absence of motile reproductive elements[1] and by the occurrence of a special type of sexual process, known as conjugation. In the vast majority of cases this consists in the fusion of the undivided protoplasts of ordinary vegetative cells. Otherwise reproduction is effected only by cell-division.

Included in the group are two series, viz. the Zygnemales in which the vegetative body consists of an unbranched filament, and the Desmidiaceae in which the habit is prevalently unicellular. The latter however comprise two sets of forms whose relation to one another is by no means clear. In the one set, the Saccoderm Desmids (*Mesotaenium*, *Cylindrocystis*, *Spirotaenia*, etc. (fig. 93)), the cell-wall is composed of a single piece, is devoid of pores, and is usually[2] readily soluble in ammoniated copper oxide; in the Placoderm Desmids, on the other hand, the cell-wall consists of two (rarely more) pieces, is generally traversed by pores, and is differentiated into two layers of which the outer is little soluble in ammoniacal copper oxide. There are other differences between these two sets of Desmids which are not so sharply defined. Thus, in the Saccodermae the chloroplasts are on the whole of a less elaborate type than in the Placodermae (cf. figs. 93 and 102), and there is a tendency for the zygospore on germination to give rise to four individuals rather than to the two customary in the Placodermae.

A fairly close affinity between the Saccoderm Desmids and the Zygnemales is apparent, but the relation of the highly specialised Placodermae to the others is by no means evident. There is no indication of how the complex wall-structure of the latter has been arrived at, and the possibility of an origin distinct from that of the other two series must be envisaged.

[1] This was the basis for the establishment of the class Akontae, but there is no reason to suppose that the Conjugatae were derived from non-motile forms. Many other Isokontae (Chlorococcales) are devoid of all motile stages at the present day.

[2] Not in *Spirotaenia* according to Lütkemüller (Verh. Zool.-Bot. Ges. Wien, LV, 1905, p. 333).

One cannot feel sure that the undoubted resemblances are not due to homoplasy. The writer is therefore unable to share wholeheartedly either the views of G. S. West (1915, p. 80; 1916 *a*, p. 331) and Lütkemüller[1] as to the close relation of Saccoderm and Placoderm Desmids, or those of Oltmanns (1922, p. 126) who regards the Mesotaeniaceae as descended from the ancestral type from which both the Zygnemales and Placoderm Desmids originated along separate lines.

It is believed that a clearer conception of the Conjugatae is obtained by the adoption of the following classification:

Series I. *Euconjugatae*: Unicellular or filamentous; cell-wall of a single piece, without obvious pores; chloroplasts usually plate-shaped, stellate, or spiral.

(*a*) *Mesotaeniales* (Saccoderm Desmids): unicellular or colonial.

(*b*) *Zygnemales*: filamentous.

Series II. *Desmidiaceae* (Placoderm Desmids): Unicellular or colonial; cell-wall of two or more pieces, generally provided with pores; chloroplasts commonly composed of a central body provided with radiating plates or processes.

In the following the three subdivisions of Conjugatae will be considered separately.

Series I. EUCONJUGATAE

(*a*) Mesotaeniales (Saccoderm Desmids)

Here are included a number of "Desmids" whose cell-structure is relatively simple and which are probably primitively unicellular, viz. *Mesotaenium* (fig. 93, D), *Roya*, *Cylindrocystis* (fig. 93, H), *Spirotaenia*, and *Netrium* (fig. 93, K). The cells are commonly rod-shaped or oblong and without a median constriction, such as occurs so commonly in the Desmids proper. The smooth cell-wall is composed of a single piece[2], and there is no evidence, direct or indirect, of the presence of pores. There is no differentiated outer layer, and the wall is usually readily soluble in an ammoniacal solution of copper oxide.

The often prolific multiplication takes place by the formation of a transverse septum approximately across the middle of the cell; this septum arises, as in *Spirogyra*, as an annular ingrowth from the longitudinal walls[3] and, by the subsequent dissolution

[1] Lütkemüller, Cohn's Beitr. VIII, 1902, p. 404.

[2] This fact can be established by careful microscopic investigation and thus a member of Mesotaeniales is readily recognised.

[3] cf. Kauffmann, Zeitschr. f. Bot. VI, 1914, p. 738; West, 1915, p. 79; Puymaly, Comptes Rendus, CLXXVI, 1923, p. 187.

of the middle lamella, the two daughter-cells separate from one another[1]. In several of the terrestrial species of *Mesotaenium* and *Cylindrocystis* large numbers of individuals are found within a common mucilage-envelope which not uncommonly shows distinct strata representing the gelatinised outer layers of the membranes of successive generations. Puymaly (loc. cit.) has recently drawn attention to the fact that in *Cylindrocystis crassa* division takes place in (two or three) successive planes at right angles to one another. This marks a more primitive condition than that encountered in Placoderm Desmids, where division always takes place in the transverse plane only, and the question of its occurrence in other Mesotaeniales is worthy of investigation.

The genera of Mesotaeniales present us with the three types of chloroplast-structure found in the cells of Zygnemales, viz. a flat plate with one or several pyrenoids in *Mesotaenium* (fig. 93, D–F), a pair of stellate chloroplasts each with a massive central pyrenoid in *Cylindrocystis* (fig. 93, H), and a spiral band twisting to the left with irregularly scattered pyrenoids in *Spirotaenia* (fig. 93, A). *Netrium* (fig. 93, K) has two chloroplasts resembling those of the Desmids proper and consisting of a central rod with a considerable number of radiating plates, often deeply notched at their edges; each chloroplast generally contains one much elongated pyrenoid. This type might have been derived from that of *Cylindrocystis* by elongation. The single nucleus is commonly found in the middle of the cell.

Sexual reproduction is of frequent occurrence in species of *Cylindrocystis* and *Mesotaenium* and has been observed in all five genera, but in *Netrium* the details are not known. In the first two genera[2] the conjugating cells, with their long axes parallel or at right angles to one another and usually embedded in mucilage, put out conjugation processes which meet end to end in the customary manner. By solution of the separating wall the conjugation canal is established and within this the contracted protoplasts meet and fuse; at the same time a marked widening of the canal takes place, so that it is no longer very sharply defined from the membranes of the conjugating cells

[1] The method of growth of the cell subsequent to the completion of division is not altogether clear. G. S. West (1916 *a*, p. 363) speaks of one half of the cell being older than the other, but in another place (Monogr. Brit. Desm., Ray Soc. 1, 1904, p. 37) we have "The individuals do not reach maturity by the mere growth of the younger half-cell, but there is a subsequent periodical growth, chiefly in length" (cf. also West, 1904, p. 154; West, 1915, p. 79; Lütkemüller, loc. cit. p. 391).

[2] De Bary, 1858, p. 30; Kauffmann, loc. cit. p. 742; West, 1915, p. 80; Hodgetts, Journ. of Bot., 1920, p. 68.

(cf. fig. 93, I). The zygote develops a thick several-layered wall and remains for a time at least surrounded by the joined membranes of the two gametes. The sexual process is altogether isogamous.

The process of conjugation just described finds a parallel in certain species of *Chlamydomonas*, where the gametes are provided with membranes and a kind of canal is established linking up the two cells prior to fusion. In fact the only intrinsic difference lies in the non-motility of the fusing individuals in a Conjugate and, as far as the process of conjugation is concerned, there is thus no difficulty in deriving the Mesotaeniales from an ancestry in common with that of other Isokontae[1].

In certain species of *Spirotaenia* (e.g. *S. condensata* Bréb.) double zygospores are regularly formed[2], and such have also been recorded as an exception in *Cylindrocystis Brebissonii*. In these cases the contents of the conjugating individuals divide into two and this is accompanied by a gradual gelatinisation of the wall until the four protoplasts are embedded in a common mass of structureless mucilage; thereupon the corresponding half-protoplasts fuse with the production of a pair of zygospores. No conjugation canals are formed in this case.

Two successive nuclear divisions (of which the first is the reduction division)[3] occur in the germination of the zygospore which takes place after a period of rest. It would appear to be the rule in the Mesotaeniales that four new individuals are constituted around these four nuclei, although only two are formed in *Spirotaenia*[4] and occasionally in *Mesotaenium*[5]. In *Cylindrocystis* the four chloroplasts of the gametes persist and are distributed to the offspring. The new cells are liberated by rupture of the zygospore-membrane.

All five genera may be placed for the present in the single

Family MESOTAENIACEAE

The key for the determination of the genera is, for the sake of convenience, included with that for the Desmidiaceae on p. 265. The British species will be easily determined with the help of W. & G. S. West's excellent monograph[6].

Spirotaenia de Brébisson, 1848[7]. Cells straight or very

[1] cf. Blackman and Tansley, 1903, p. 45.

[2] Archer, Quart. Journ. Microscop. Sci. VII, 1867, p. 186; Lütkemüller, Österr. Bot. Zeitschr. XLV, 1895, p. 91.

[3] Kauffmann, loc. cit. p. 756.

[4] Kauffmann, loc. cit. p. 765.

[5] West, 1915, p. 80.

[6] Ray Soc. I, 1904.

[7] Archer, loc. cit.; Lütkemüller, Österr. Bot. Zeitschr. XLV, 1895, p. 1, and LIII, 1905, p. 396.

slightly curved, oblong-cylindrical or fusiform, with rounded, truncate, subacute, or acute apices, frequently enveloped in mucilage. Chloropl. single, with one or many pyrens., always spirally twisted to the left, either parietal (sect. Monotaenieae

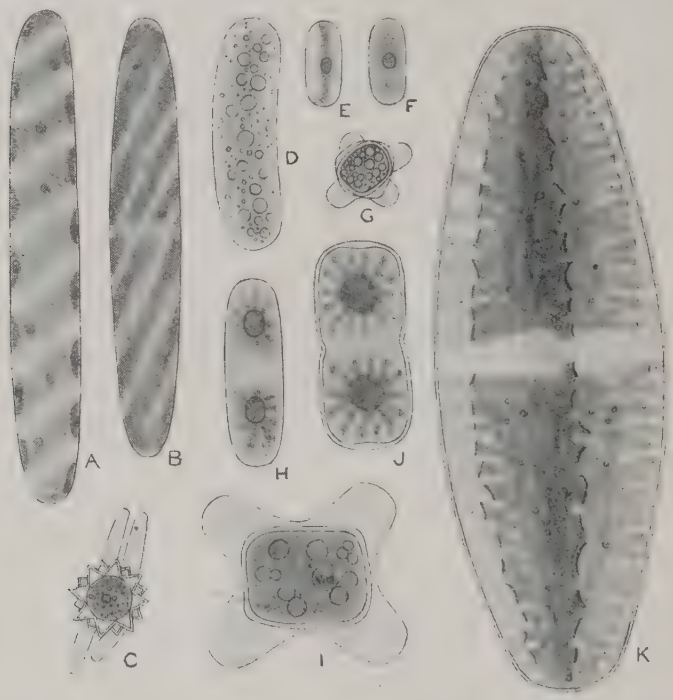

Fig. 93. A, *Spirotaenia condensata* Bréb., from Rhiconich, Sutherland (×334), showing parietal chloroplast. B, *S. obscura* Ralfs, from Terrington, N. Yorks (×435), showing the axile, cristate chloroplast. C, zygospore of *S. truncata* Arch. (×250, after Archer). D, *Mesotaenium De Greyi* Turn., from near Settle, W. Yorks (×435). E and F, *M. macrococcum* (Kütz.) Roy and Biss., from near Giggleswick, W. Yorks (×334). G, zygospore of *M. chlamydosporum* De Bary, from Mayo, Ireland (×334). H and I, *Cylindrocystis Brebissonii* Menegh., from Helvellyn, Cumberland; H, vegetative cell; I, zygospore (×435). J, *Cosmarium diplosporum* (Lund.) Lütkem., from Galway, Ireland (×435). K, *Netrium Digitus* (Ehrenb.) Itzigs. and Rothe, from Moel Siabod, N. Wales (×435).

Rabenh.) (fig. 93, A) or axile with a variable number of spirally twisted ridges (sect. Polytaenieae Rabenh.) (fig. 93, B); nucleus excentric. Double zygosp. frequently produced.

There are 14 Brit. sp., mostly occurring in peat-bogs, but none is common. *S. condensata* Bréb. (18–27 br.; 150–270 l.) (fig. 93, A)

is the largest and most widely distributed, and *S. closteridia* (Bréb.) Arch. is the smallest (4·5 4·6 br.; 13·5 l.). All the sp. are very delicate with thin cell-walls, and most of them can only be identified with certainty from living specimens. The zygosp. are rarely met with and usually have an ornamented surface (fig. 93, C).

Mesotaenium Naegeli, 1849[1] (*Palmogloea* Kützing, 1843). Cells cylindrical or subcylindrical, often in large numbers within a mass of mucilage, straight or slightly curved, apices usually broadly rounded. Chloropl. single (rarely two), a flattened axile plate extending from end to end of the cell and with one or several pyrens.: cells often with numerous oil-globules; nucleus very small, median, adpressed to the chloropl. Zygosp. generally polyhedral with thick brown walls yielding four or two individuals on germination.

Seven of the ten Brit. sp. occur as mucilaginous masses amongst Mosses and Hepatics, generally on wet rocks. The largest of these is *M. De Greyi* Turn. (15·5–30 br.; 74–125 l.) (fig. 93, D) and the smallest *M. macrococcum* (Kütz.) Roy and Biss. var. *micrococcum* (Kütz.) W. & G. S. West (8·6 br.; 13·5–15·3 l.). *M. caldariorum* (Lagerh.) Hansg. (10·5–11·5 br.; 27–46 l.) is an attenuated sp. occurring in greenhouses as a thin mucous stratum on damp walls, etc., and is also recorded under trees in Wyre Forest. *M. purpureum* W. & G. S. West and *M. violascens* De Bary contain phycoporphyrin, the latter being not uncommon on the soil of heaths in the South of England. *M. Endlicherianum* Naeg. (8·5–9·5 br.; 25–27 l.) is the most frequent of the free-floating forms.

Cylindrocystis Meneghini, 1838[2]. Cells straight, cylindrical, usually about twice as long as wide, apices rounded or truncately rounded. Chloropl. axile, one in each half of the cell, substellate, with a large central pyren. and a varying number of radiating prolongations often flattened at the periphery. Zygosp. quadrangular or spherical, yielding four individuals on germination; parthenospores also observed[3].

Of the five Brit. sp. the most abundant is *C. Brebissonii* Menegh. (15–18 br.; 43–55 l.) (fig. 93, H and I), which is found in quantity in upland *Sphagnum*-bogs and in peaty pools. It sometimes occurs in pure masses both amongst *Sphagnum* and on wet peat. *C. crassa* De Bary is also found in *Sphagnum*-bogs and amongst other Algae and Mosses on wet rocks; occasionally it inhabits damp soil.

[1] Naegeli, 1849, p. 108; De Bary, 1858, p. 30; West, 1915, p. 78.

[2] Lütkemüller, Verh. Zool.-Bot. Ges. Wien, LXIII, 1913, p. 212; De Bary, 1858, p. 35; Kauffmann, loc. cit.

[3] cf. Borge, Bot. Notiser, 1913, p. 8.

Netrium Naegeli, 1849; emend. Lütkemüller, 1902[1]. Cells straight, cylindrical, oblong-cylindrical, or fusiform. Chloropl. two in each cell (four in one sp.), composed of an axile rod with 7–12 radiating longit. plates, usually deeply notched along their free edges (except *N. interruptum*); usually a single much elongated pyren., surrounded by a thick sheath of starch, in each chloropl. Zygosp. spherical, smooth.

N. Digitus (Ehrenb.) Itzigs. and Rothe is one of the most abundant Desmids of elevated boggy moorlands and varies much in form and size (40–82 br.; 130–387 l.) (fig. 93, K). *N. oblongum* (De Bary) Lütkem. occurs in similar situations, but is not quite so frequent: cells 32–33 br. and 96–135 l. *N. interruptum* (Bréb.) Lütkem. is cylindrical with obtusely conical apices and each chloropl. is transv. divided, so that there are four chloropl. arranged in an axile series; cells 37–64 br. and 220–320 l.

Roya W. & G. S. West, 1896; emend. Hodgetts, 1920[2]. Cells elongate, cylindrical, straight or slightly curved, sometimes gently attenuated towards the more or less truncate or obtusely rounded apices. Chloropl. one in each cell, axile, with a small number of longit. ridges and a median series of pyrens. (4–13), either extending to the apices of the cells or the latter occupied by terminal vacuoles without moving granules; in older cells the chloropl. may be divided at the middle. Nucleus lateral, lodged in a small bay of the chloropl., or median between the two halves of the latter. Zygosp. globose and smooth.

The genus is easily distinguished from *Closterium* (p. 269) by the absence of any marked attenuation towards the apices, the cell-wall composed of a single piece, and the usually single chloropl.

All four sp. occur in Britain. *R. obtusa* (Bréb.) W. & G. S. West and its var. *montana* (fig. 105, G and H, p. 268) are not uncommon in mountainous districts; cells 5·5 12·5 br. and 48–117 l. *R. Pseudoclosterium* (Roy) W. & G. S. West is a very narrow sp. (2·6–3 br.; 98 192 l.) (fig. 105, J. and K) of rare occurrence. *R. Cambrica* W. & G. S. West (6·2–6·7 br.; 173–177 l.) (fig. 105, I) is only known from N. Wales. *R. anglica* West differs from all these in the possession of vacuoles in the apices of the cells.

[1] Naegeli, 1849, p. 107; Lütkemüller, Beitr. z. Biol. d. Pfl. VIII, 1902, p. 404; Carter, Ann. of Bot. XXXIII, 1919, p. 227.

[2] W. & G. S. West, Journ. Roy. Microscop. Soc., 1896, p. 152; Lütkemüller, Verhandl. Zool.-Bot. Ges. Wien, LX, 1910, p. 479; Hodgetts, Journ. of Bot. LVIII, 1920, p. 65.

(*b*) Zygnemales

The Zygnemales comprise a number of the commonest filamentous freshwater Algae, all of them unbranched[1]. They favour more particularly smaller stagnant pieces of water and are specially abundant in the spring months. In their natural habitats they withstand extremes of temperature very well, and they seem capable of adapting themselves to very diverse conditions. They usually occur as bright green free-floating masses, but some kind of attaching organ is present in young stages in several genera and there are a few species of *Spirogyra* that occur permanently attached in flowing water. Otherwise there is no differentiation among the cylindrical cells. In several genera dissociation of the threads into separate cells readily occurs, a feature which is especially pronounced in the Gonatozygaceae.

The chloroplasts are essentially of the same three types as were noted in the Mesotaeniales, viz. a flat plate (*Mougeotia* (fig. 100, C), *Debarya*), a pair of stellate chloroplasts (*Zygnema* (fig. 97, A)), or one or more spiral bands twisting to the left (*Genicularia* (fig. 95, I)) or right (*Spirogyra* (fig. 98), *Sirogonium*); for details see under the genera. The more complex type of *Netrium* is not paralleled in this group. The single nucleus is nearly always situated in the middle of the cell, being apposed to one side of the chloroplast in *Mougeotia*. Its structure and division have been much studied[2], but a consideration of these matters is outside the scope of this work; the bulk of the chromatin is often contained in the nucleolus and the spindles are intranuclear. Palla[3] first drew attention to the frequent occurrence in the cells of diverse genera of small protein-bodies (caryoids), the function of which is not yet ascertained.

The cell-wall is composed of a single piece, is usually moderately thin, and generally provided with a more or less conspicuous pectose mucilage-sheath to which the Zygnemales owe their slimy feeling. With appropriate stains (e.g. methyl violet) a fibrillar structure of the mucous envelope[4], perpendicular to the

[1] In *Zygnema* and *Mougeotia* branches in the shape of short lateral outgrowths, consisting only of a few cells, are very occasionally observed (West and West, 1898, t. IV, figs. 17, 18, 19 and 41).

[2] See esp. Moll, Verhandl. K. Akad. Wetensch. Amsterdam, 2 sect., No. 9, 1893; Berghs, La Cellule, xxiii, 1906, p. 55; Escoyez, La Cellule, xxiv, 1907, p. 355; Merriman, Bot. Gaz. xli, 1906, p. 43, and lvi, 1913, p. 319; Tröndle, Zeitschr. f. Bot. iv, 1912, p. 721; Peterschilka, Arch. f. Protistenk. xlv, 1922, p. 153, and xlvi, 1923, p. 153; Czurda, ibid. xlv, 1922, p. 163.

[3] Palla, Ber. Deutsch. Bot. Ges. xii, 1894, p. 153.

[4] Klebs, Unters. Bot. Inst. Tübingen, ii, 1888, p. 336.

surface, can be detected and, although this suggests an excretion of mucilage through pores in the wall, such pores have not as yet been demonstrated by anyone. In the longitudinal walls it is possible to distinguish a superficial "cuticle" and inner layers consisting mainly of cellulose.

The transverse walls, which are formed by annular ingrowth during cell-division, frequently show a more or less complex structure which is related to the ready fragmentation of the filaments[1]. In many cases, of which *Mougeotia* furnishes a particularly good example, the septa at an early stage split into two circular discs unconnected with one another but continuous with the longitudinal walls of their appropriate cells which are henceforth held together only by the cuticle; the two parts of the septum frequently bulge apart, so that the latter appears biconvex. In the species of *Spirogyra* with "replicate" end-walls (fig. 94, C and D) the middle lamella of the septum develops on either side a cylindrical ring-like ingrowth (resembling a collar) over which the subsequent apposition-layers are deposited; by the dissolution of the middle lamella the cells are again left connected only by the cuticle. In this case the ingrowth becomes evaginated when the cells break apart, so that the detached cell has a characteristic rounded extremity. Rupture of the threads in these different cases is probably usually brought about by an alteration in the turgor of one or other cell.

Akinetes are formed in *Mougeotia* and specially commonly in *Zygnema*. A high altitude, which is usually accompanied by a relatively low temperature, favours their production. In shape they mostly differ but little from the vegetative cells, but the walls become markedly thickened, whilst starch and fat accumulate within the protoplast. Not uncommonly threads producing such akinetes are encased in a prominent mucilage-envelope, even when none is evident around the ordinary filaments. The cells of the terrestrial form of *Zygogonium ericetorum* may be said to exist permanently in the akinete-condition (cf. p. 248).

The majority of the Zygnemales readily conjugate and, since specific differences are largely based on the characters of the conjugating cells and of the resulting zygospores, sterile material belonging to members of this group is nearly always indeterminable. Moreover, the genera *Debarya* and *Mougeotia* are indistinguishable except in the fertile condition. In the British Islands conjugating examples are more frequently met with in low-lying areas than in upland districts and most frequently in the western

[1] Benecke, Jahrb. Wiss. Bot. XXXII, 1898, p. 453.

and south-western counties. Conjugation occurs mainly between February and June[1].

The conjugation-process[2] usually takes place between two filaments[3] which become ranged parallel to one another. In *Spirogyra* Czurda states that the threads are intimately glued together by the gelatinised outer layers of the walls. This is followed by the putting out of conjugation-processes from opposite cells, the protuberances at the same level exactly corresponding and growing towards one another till they meet; in *Spirogyra*, according to Czurda, the lengthening processes push the filaments apart. The separating walls are then dissolved, so that an open, usually relatively narrow, conjugation-tube is established; the gametes are in contact from the first. The contraction of their protoplasts is heralded in *Spirogyra*, and probably in other cases too, by a reduction in turgor. In some species conjugating cells are shorter than the vegetative ones.

In *Debarya* and some species of *Zygnema* the gametes meet in the conjugation-tube, so that the process is both morphologically and physiologically isogamous (cf. figs. 96, 97, F). In other species of *Zygnema* and in *Spirogyra*, however, fusion takes place in one of the two gametangia (cf. fig. 94), so that the one gamete (the female) is passive and the other (the male) relatively active[4]. Usually all the cells of a filament behave alike and all the zygospores are lodged in the one (the female) filament[5]. The anisogamy is however purely a physiological one, since the gametes are not morphologically distinct. The difference between the two filaments becomes early apparent, since the cells of the male put out conjugation-processes and undergo contraction of their protoplasts to form the gametes a little time before the same changes are observed in the female filaments. That part of the conjugation-tube developed from the female cell is usually thicker and shorter than the part developed from the male. The female cells frequently become much swollen after the fusion of the gametes.

According to Lloyd (loc. cit.) the contraction of the gametes

[1] cf. Fritsch and Rich, Ann. of Bot. xxi, 1907, p. 423; Hodgetts, 1921, p. 17.

[2] cf. De Bary, 1858, pp. 3, 11, 21, etc.; Klebs, 1896, p. 229; W. and G. S. West, 1898, p. 36; Lloyd, Trans. Roy. Canadian Inst., Toronto, xv, 1924, p. 129; Czurda, Archiv f. Protistenk. li, 1925, p. 439.

[3] Three, four, five, six, or more are occasionally involved (cf. fig. 94, A); cf. also Brown, Bot. Gaz. lxvi, 1918, p. 269.

[4] According to Kurssanow (Flora, civ, 1912, p. 66) the male gamete of *Zygnema* rotates through 90° before passing into the conjugation-canal.

[5] Cross-conjugation, in which some cells of the filaments are male and others female, so that perfectly normal zygospores are found in both threads, is exceedingly rare.

is due to the discharge of liquid from a number of large, nearly spherical, contractile vacuoles which appear sooner in the male than the female and are also operative in bringing about the final contraction of the zygote: it will be of interest to ascertain whether these and other features described by Lloyd, so far only for a single species, are of more general application.

Irregularities in the conjugation-process are occasionally observed. Zygospores are sometimes produced by the coalescence of three gametes, two male and one female[1], but attempts of this nature are usually abortive (fig. 94, B)[2]. Gerassimoff observed conjugation of two female cells with one male cell, one of the former producing a parthenospore[3].

The ladder-like or scalariform method of conjugation described above is that habitual in *Spirogyra* and *Zygnema*, but in both another method (lateral conjugation) is occasionally observed and in some species of *Spirogyra* (e.g. *S. affinis*, *S. tenuissima*) may even be the rule. In this case there is no sexual differentiation between the filaments, and the conjugation-processes arise from adjacent ends of neighbouring cells, between which an open conjugation-tube is thus established[4] (fig. 94, D): the zygospore lies either in the canal or in one of the conjugating cells, according as the gametes are "isogamous" or "anisogamous." The same filament may sometimes show both scalariform and lateral conjugation. The latter is very rare in the Mougeotiaceae.

In the remaining genera of Zygnemales various specialisations in the conjugation-process are apparent. In *Mougeotia* the gametes are produced from only a part (incl. the nucleus and chloroplast) of the protoplast of the gametangium. After fusion within the conjugation-canal the compact zygote is not immediately cut off from the cytoplasm left in the gametangia; but soon variously orientated walls arise separating it from the surrounding sterile parts, which then appear as two (fig. 100, F), three, or four (fig. 100, I) cells. It is peculiar to this genus that these remains of the gametangia persist around the mature zygospore. *Mougeotia* is thus isogamous, but it may be noted that the zygospores are often seen to be situated nearer to one of the conjugating cells, whose conjugation-tube is thicker and shorter than that of the other. This is especially marked in

[1] West, Notarisia, VI, 1891, t. XIII, fig. 13; Borge, Bih. K. Sv. Vet.-Akad. Handl. XVII, 1891, Afd. III, No. 2, t. I, fig. 2; W. and G. S. West, 1898, t. V, fig. 66.

[2] W. and G. S. West, 1898, figs. 67 and 69; Schmula, Hedwigia, XXXVIII, 1899, p. (1).

[3] Gerassimoff, Bull. soc. imp. nat. Moscou, 1897, p. 494.

[4] Regarding its mode of formation see Lloyd, p. 130, and Czurda, p. 472.

Fig. 94. A, *Spirogyra nitida* (Dillw.) Link, from near Morecambe, Lancs; scalariform conjugation between six filaments (×75). B, *S. setiformis* (Roth) Kütz., showing frustrated attempts at the conjugation of two male cells and one female cell (×90). C, *S. Spreeiana* Rabenh., from near Esher, Surrey (×390). D, *S. inflata* (Vauch.) Rabenh., from near Esher, Surrey; showing lateral conjugation (×390). E and F, zygospores of *S. velata* Nordst., from Shipley Glen, W. Yorks, germinating immediately after their formation and before the differentiation of the wall of the zygospore (×165). G, germination of zygospore of *S. velata* after normal period of rest (×230).

M. tenuis (Cleve) Wittr., where the zygospore is located mainly in one of the two conjugating cells.

In *Zygogonium*[1] the gametes are again produced only from part of the protoplasm of the gametangia. Before the canal is fully established, the greater part of the protoplast passes into the conjugation-process and becomes cut off by a curved wall (fig. 99, D); within the cell thus formed the gamete secretes an independent thin membrane and, after the fusion of the gametes, these membranes unite to form the outermost layer of the zygospore-wall (fig. 99, E, F).

In *Temnogametum*[2], which has the vegetative characters of a *Mougeotia* and is so far only known from Tropical Africa and Brazil, the cells before conjugation divide to form a large sterile and a small fertile one. The fertile cells become approximated without the formation of a tube, but there is no contraction of their contents and after fusion the zygospore occupies them jointly. Lateral conjugation also occurs.

Morphological anisogamy is found only in *Sirogonium*[3] (*Choaspis* (fig. 99, A–C)) which in vegetative habit closely resembles *Spirogyra*, although the chloroplasts run almost longitudinally. The approximation of the conjugating cells takes place mainly by bending, especially of the female cell, and no distinct conjugation-tubes are formed; at the point of contact of the two cells there is a ring of mucilage. Preparatory divisions take place, whereby two gametes of different sizes are produced (fig. 99, A). In the male a first division separates off a small sterile cell at one end, after which a second much larger sterile cell is cut off at the other end; in the female cell of the opposite filament there is only one division separating a small sterile cell, so that the resulting female gamete is much larger than the male. The zygospore forms in the female cell (fig. 99, B).

The ripe zygospores are usually spherical or ellipsoidal and in most cases possess a thick wall which is composed mainly of cellulose and is divisible into three layers, the outer being cuticularised and the middle one often exhibiting distinctive markings (fig. 96, B, E). The contents of the zygospore commonly turn red and accumulate a large amount of oily material. Sometimes the chloroplasts of the two gametes remain intact in the zygospore up to late stages (e.g. *Zygnema*); more usually in *Spirogyra* those of the female remain, while those of the male disintegrate[4]. According to G. S. West (1904, p. 126; 1916 *a*,

[1] Hodgetts, New Phytol. XVII, 1918, p. 238.

[2] W. and G. S. West, Journ. of Bot., 1897, p. 12.

[3] De Bary, 1858, p. 13.

[4] Chmielevsky, Bot. Zeit. XLVIII, 1890, p. 773; Tröndle, ibid. LXV, 1907, p. 196.

p. 350), however, it is quite a common thing for the chloroplasts to disintegrate completely before the fusion of the gametes.

It frequently happens in nature that conjugation is brought to an abrupt termination. In such cases the spores are apt to be very variable, either not exhibiting the typical form or a small one is formed in each gametangium or two small ones in the female cell[1]. In several genera of Zygnemales parthenogenesis occurs as an occasional phenomenon. The simplest case is constituted by *Spirogyra groenlandica*[2] in which, after the conjugation-processes have met but usually before the establishment of an open tube, the contents of the gametangia round off and, secreting a membrane, become "azygospores" (parthenospores). Much the same obtains in *Mougeotia*[3] and in *Zygogonium*[4]. Klebs (1896, p. 247) was able to bring about the formation of azygospores artificially in *Spirogyra varians*, a species which in nature always exhibits normal conjugation, by placing conjugating filaments in a strong solution of sugar. In *S. mirabilis* (Hass.) Kütz.[5] there is no indication even of the preliminaries of the conjugation-process, the azygospores being simply formed by marked contraction and rounding off of the contents of the cells[6]. *Zygnema spontaneum* Nordst. at times behaves similarly, but at others exhibits normal scalariform conjugation[7].

Formation of such parthenospores is also a perfectly normal phenomenon in *Gonatonema*[3] whose vegetative structure is like that of *Mougeotia*. In this case the protoplast contracts to the somewhat enlarged middle portion of the cell which becomes cut off by septa from the empty parts; the spore then develops a special wall of its own (fig. 101). Not uncommonly the cells concerned exhibit a knee-like bending, similar to that often shown by conjugating cells of *Mougeotia*.

Nuclear fusion is postponed for some little time after the

[1] Kolderup-Rosenvinge, Öfvers. K. Sv. Vet.-Ak. Förhandl. XL, 1883, No. 8, t. VIII; West, Notarisia, VI, 1891, t. XIII, figs. 27, 28; Hansgirg, Hedwigia, XXVII, 1888, t. X, fig. 6; W. and G. S. West, 1898, t. V, figs. 74–80.

[2] Kolderup-Rosenvinge, loc. cit. p. 37.

[3] Wittrock, Bih. K. Sv. Vet.-Ak. Handl. v, 1878, No. 5.

[4] Hodgetts, loc. cit. p. 247.

[5] Hassall, 1845, p. 156; Klebs, 1896, p. 254.

[6] Petit (*Spirogyra* d. environs d. Paris, 1880, p. 14) states that the formation of these spores is preceded by a separation of the contents of the cell into two parts which later fuse to form the spore, but this has not been confirmed by later work (Klebs, Peterschilka, see p. 245). A somewhat analogous phenomenon has been described by G. S. West in *Gonatonema* (cf. p. 251). Possibly in these cases there is some relation to lateral conjugation.

[7] Nordstedt, De Algis aquae dulcis, etc. ex insula Sandvicensibus reportatis, Lund, 1878, p. 17; W. and G. S. West, Journ. of Bot., 1897, p. 15.

amalgamation of the gametes. Reduction division takes place in the majority of cases soon after, during the ripening of the zygospore, but in *Spirogyra jugalis* and *S. communis* it only occurs just before germination as in Mesotaeniales and Desmidiaceae[1]. Of the four nuclei produced one enlarges, whilst the others gradually abort, a single individual resulting from each zygospore[2]. As a preliminary to germination the abundant oil is converted to starch, whilst the chloroplasts become more distinct. Thereupon the thick membrane is burst at one end and the contents, surrounded by an inner layer, grow out as a long tube which soon undergoes division into two cells (fig. 94, G). The lower of these has scanty chlorophyll and often appears colourless for a great part of its length and, in *Spirogyra* and *Mougeotia*, it may develop into a definite rhizoid; the upper proceeds to divide to form the thread. In *Zygnema* the distinction into base and apex is scarcely evident.

Since filaments of diverse species of Zygnemales often occur intermingled with one another, the production of hybrids is not altogether rare[3]. Cases have been observed both in *Spirogyra* and *Mougeotia*, but no detailed work on this subject has so far been done.

The classification of Zygnemales presents considerable difficulties. The older grouping into Mesocarpaceae and Zygnemaceae, which was based upon the peculiar method of zygospore-formation in the former, is not easily maintained. In his last work G. S. West (1916 *a*, p. 331) advocated a classification depending on the characters of the chloroplast, but this creates the difficulty of finding a suitable place for *Pleurodiscus*[4] and *Zygogonium* whose chloroplasts do not conform to one of the three main types, besides obviously being very artificial.

It is believed that a way out of the difficulty may be found by separating *Debarya*, *Zygnema*, and *Spirogyra* (also *Pyxispora*)[5], in which the zygospore is formed without preparatory or subsequent division of the conjugating cells, from the other genera. The divisions taking place in *Sirogonium*, *Temnogametum*, and *Zygogonium* prior to conjugation are regarded as comparable to those occurring in *Mougeotia* subsequent to conjugation. The two families are described as Zygnemaceae and Mougeotiaceae,

[1] Karsten, Flora, XCIX, 1908, p. 1; Tröndle, Zeitschr. f. Bot. III, 1911, p. 593.

[2] cf. however Kolderup-Rosenvinge, Rev. Algol. I, 1924, p. 209.

[3] W. and G. S. West, 1898, t. V, figs. 70, 71; Bessey, Amer. Naturalist, XVIII, 1884, p. 67; Andrews, Bull. Torrey Bot. Club, XXXVIII, 1911, p. 299; Transeau, Amer. Naturalist, LIII, 1919, p. 109.

[4] cf. Lagerheim, Vidensk. Selsk. Skrift., Mat.-nat. Kl., 1895, No. 5, p. 7.

[5] W. and G. S. West, Journ. of Bot., 1897, p. 14.

it being deemed advisable to discontinue the old name Mesocarpaceae, even at the expense of a more clumsy substitute. With reference to the two genera *Gonatozygon* and *Genicularia*, Oltmanns (1922, p. 97) has been followed in placing them among Zygnemales which they resemble in the production of a single embryo from the zygospore. They certainly do not fit well into the Desmids, nor into the Mesotaeniales, and they are here regarded as reduced Zygnemales.

The following key will serve to determine the British genera of Zygnemales:

A. Cells elongate, joined to form loose threads which easily dissociate into the individual cells, as always prior to conjug.; wall of a hyaline inner portion and an outer layer which is usually rough or provided with minute spines *Gonatozygaceae*
- *a*. Chloropl. axile *Gonatozygon*
- *b*. Chloropl. parietal and spirally twisted *Genicularia*

B. Cells of varying length forming threads which do not dissociate prior to conjugation; wall smooth, with an outer mucilage-envelope
- *a*. No divisions take place in the cells preparatory or subsequent to conjug. *Zygnemaceae*
  1. Chloropl. one per cell, a flat plate, zygosp. in conjug. canal *Debarya*
  2. Chloropl. two per cell, stellate, zygosp. in canal or in one of the conjug. cells *Zygnema*
  3. Chloropl. 1–7, sometimes up to 12 per cell, spiral, zygosp. in one of the conjug. cells *Spirogyra*
- *b*. Conjug. cells either produced by certain preparatory divisions or cut off from the zygote subsequent to conjug. *Mougeotiaceae*
  1. Spores normally formed by conjug.
     - * Conjug. cells cut off prior to conjug.
       - † Chloropl. single, axile, constricted in the middle, gametes cut off from parent-cells after entering conjug. tube, zygosp. in canal *Zygogonium*
       - †† Chloropl. several, band-shaped as in *Spirogyra*, longit., male and female cells of unequal size, cut off by preparatory divisions, zygosp. in female cell *Sirogonium*
     - ** Conjug. cells cut off from zygote subsequent to conjug., zygosp. in canal, chloropl. a flat plate *Mougeotia*
  2. Spores formed without conjug. by contraction of protoplast to centre of cell, chloropl. a flat plate *Gonatonema*

Family 1. GONATOZYGACEAE

The cells are long and cylindrical and loosely joined by their apices into fragile filaments of variable length. These easily break up without interfering with the life of the individual

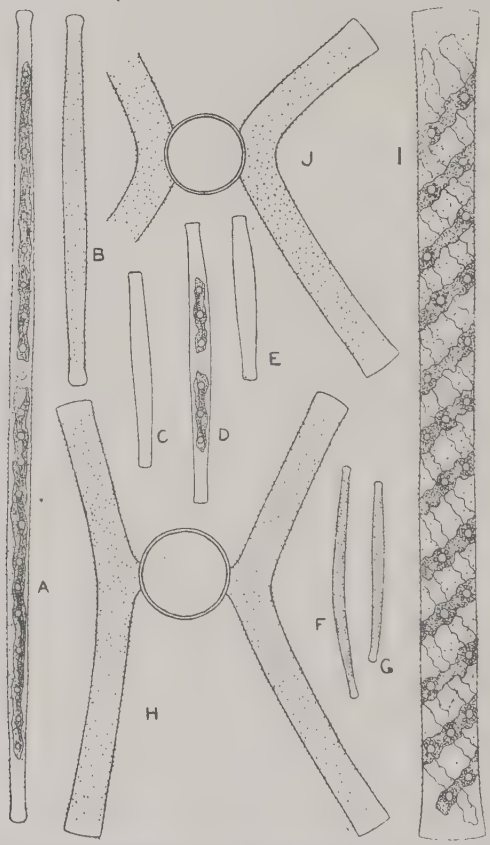

Fig. 95. A and B, *Gonatozygon Brebissonii* De Bary (×464); A, from Esher Common, Surrey; B, from Strensall, N. Yorks. C–E, *G. Brebissonii* var. *laeve* (Hilse) W. & G. S. West, from Mickle Fell, N. Yorks (×356). F and G, *G. Brebissonii* var. *minutum* W. & G. S. West, from Riccall Common, E. Yorks (×464). H, zygospore of *G. monotaenium* De Bary (×464). I and J, *Genicularia Spirotaenia* De Bary, from near the Lizard, Cornwall; I, vegetative cell (×312); J, zygospore (×220).

cells. The wall is differentiated into an inner hyaline and structureless layer and an outer layer usually provided with minute granules or small spines. Conjugation is isogamous and only

takes place between dissociated cells which usually become geniculate (fig. 95, H, J). The zygospores are smooth and spherical.

Gonatozygon De Bary, 1856. Cells cylindrical or narrowly fusiform, 10–20 (rarely 40) times as long as broad, with more or less truncate, occasionally subcapitate apices; cell-wall rarely smooth, usually covered with minute granules or short spines. Chloropl. axile, generally two in each cell (rarely only one), each a rather narrow undulated band containing 4–16 equidistant pyrens.; an apical vacuole with moving granules occasionally present at either end of the cell.

There are five Brit. sp., of which *G. monotaenium* De Bary (*G. Ralfsii* De Bary) (fig. 95, H) and *G. Brebissonii* De Bary (? *Docidium asperum* Bréb.) (fig. 95, A and B) are the most abundant. Smooth varieties of both are known (cf. fig. 95, C–E), and *G. Kinahani* (Arch.) Rabenh., the largest sp. (11–14 br.; 162–376 l.), is always smooth. The smallest form is *G. Brebissonii* var. *minutum* W. & G. S. West (fig. 95, F and G) which is 4·2–7 br. and 47·5–67·5 l.

Genicularia De Bary, 1858[1]. Cells similar to those of *Gonatozygon*[2], cylindrical with truncate apices and a rough wall. Chloropl. parietal, two or three per cell, disposed as spiral bands or rarely somewhat irregular, each with a number of pyrens.

This is one of the rarest genera of "Desmids." *G. Spirotaenia* (fig. 95, I and J) has only been found in Cornwall and the Shetlands; cells 20–25 br., 200–400 l.; zygosp. 48–57 br. *G. elegans* W. & G. S. West is a more slender sp. (14–16·3 br.; 303–427 l.) in which the chloropl. forms laxer spirals. It is known from the plankton of various British lakes.

Family 2. ZYGNEMACEAE

In this family of simple filamentous forms conjugation takes place between the ordinary cells without previous special divisions, and the zygospore lies freely within the composite structure formed of the membranes of the conjugating cells (gametangia) and the conjugation-tube. The entire protoplasm of the gametangia is utilised in the production of the gametes. The zygospore is located either in the canal or in one of the conjugating cells.

Debarya Wittrock, 1872[3] (*Mougeotiopsis* Palla, 1894). Filaments with or without distinct constriction between the elongated cells, with a thin mucous envelope. Chloropl. a single

[1] De Bary, 1858, pp. 26, 77.

[2] Wille (1909, p. 8) includes *Genicularia* in *Gonatozygon*.

[3] West and West, 1903, p. 39; Price, New Phytol. x, 1911, p. 87, and xi, 1912, p. 60.

axile plate, extending from end to end of the cell or only occupying the median portion; pyrens. several, usually arranged in a single series, rarely absent. Conjug. scalariform, the zygosp.

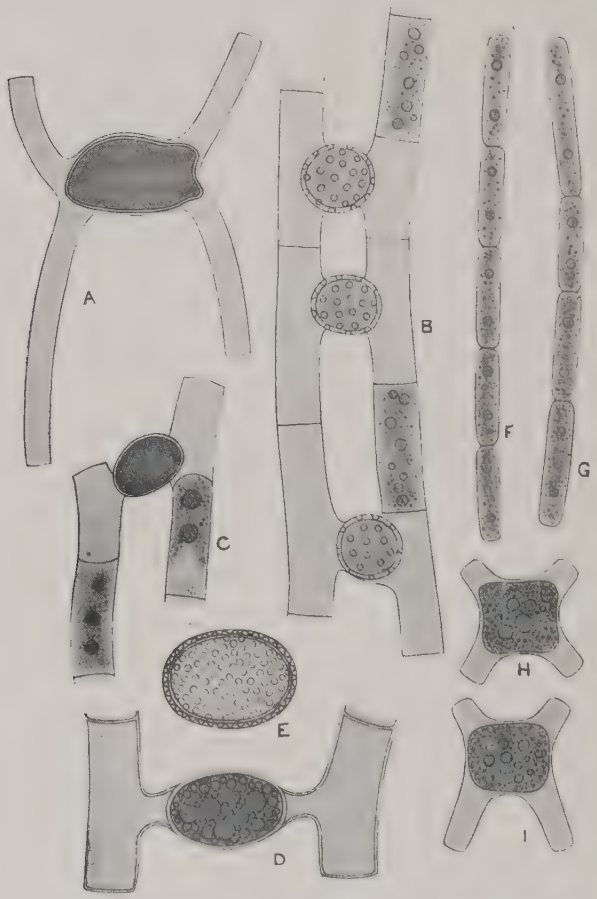

Fig. 96. A, *Debarya glyptosperma* (De Bary) Wittr., from Fairfield, Westmorland (×275). B, *D. calospora* (Palla) W. & G. S. West, from Pilmoor, N. Yorks (×430). C–E, *D. laevis* (Kütz.) W. & G. S. West, from Mitcham Common, Surrey; C, ×180; D ×250; E, mature zygospore, ×430. F–I. *D. Desmidioides* W. & G. S. West, from near the Lizard, Cornwall (×430).

formed in the tube. The mature zygosp. are very variable, and there are considerable differences in the actual processes of conjugation, but all sp. agree in the fact that, as the zygosp. is being formed, the gametangia become very clear-looking and

refractive, a series of striations being sometimes visible parallel to the transverse walls. The appearance of solidity thus acquired is probably due to the deposition of stratified mucilage inside the wall on the receding of the protoplast during conjug. This feature is noticeable even in old preserved material.

All the five sp. known from the Brit. Isles are of rare occurrence. *D. glyptosperma* (De Bary) Wittr., with cells 9–15 br. and 6–15 times as long, is the most widely distributed; the conjug.-tubes are often very long and the zygosp. (16–40 br.; 35–72 l.) is ellipsoidal, frequently with one or two mammillate protuberances at the poles (fig. 96, A). *D. laevis* (Kütz.) W. & G. S. West has larger and shorter cells (20–26 br. and $2\frac{1}{2}$–4 times as long) and the zygosp. is ellipsoidal (44–50 × 29–36) with a scrobiculate middle coat (fig. 96, C–E). *D. calospora* (Palla) W. & G. S. West is 11–13 br. and the subglobose or ellipsoidal zygosp. (18–26 br.) are ornamented with large scrobiculations (fig. 96, B). Palla[1] established for this sp. the genus *Mougeotiopsis* owing to the absence of pyrens. Subsequently, however, precisely the same sp. was discovered with pyrens., whose presence or absence cannot therefore be of generic value[2]. The most remarkable sp. of *Debarya* is *D. Desmidioides* W. & G. S. West, so far only known from Cornwall; there are distinct constrictions between its short cells (7·7–8·6 br. and $2\frac{1}{2}$–$6\frac{1}{2}$ times as long) and the filaments dissociate with great ease into the individual cells, conjug. only occurring in this condition (fig. 96, F–I). Messrs West regarded this plant as throwing much light on the origin of the Desmidiaceae; there is undoubtedly a very close relationship with *Mesotaenium*. *D. cruciata* Price is a closely allied sp.

Zygnema Agardh, 1824[3] (*Zygogonium* Kützing, 1843 pro parte). Filaments occasionally exhibiting a slight constriction between the cells, often provided with a mucilage-envelope which is sometimes remarkable for its size and strength. Chloropl. two per cell, suspended in the median line, star-shaped, sometimes rather indefinite, each with a single large pyren.; nucleus between the two chloropl. Conjug. lateral or scalariform, the zygosp. either in the canal or more commonly in the female cell. Zygosp. globose or ellipsoid.

There are about a dozen Brit. sp., of which *Z. pectinatum* (Vauch.) Ag., *Z. cruciatum* (Vauch.) Ag., and *Z. insigne* (Hass.) Kütz. (fig. 97, E) are the three largest, usually occurring in ponds or in roadside ditches. The first of these forms its zygosp. in the canal, the other two in the female cell; in *Z. insigne* the middle layer of the zygosp. membrane is smooth and brown, whilst in the other two it is scrobiculate. The smallest form is *Z. Vaucherii* Ag. var. *stagnale* (Hass.)

[1] Ber. Deutsch. Bot. Ges. XII, 1894, p. 228.
[2] W. and G. S. West, 1898, p. 49, and Journ. of Bot., 1900, p. 289.
[3] De Bary, 1858, p. 8; Kurssanow, Flora, CIV, 1912, p. 65.

Kirchn. (fig. 97, B), the filaments of which reach a max. breadth of 13 μ. Z. *anomalum* (Hass.) Cooke[1], largely confined to upland bogs, is remarkable for its wide mucous investment.

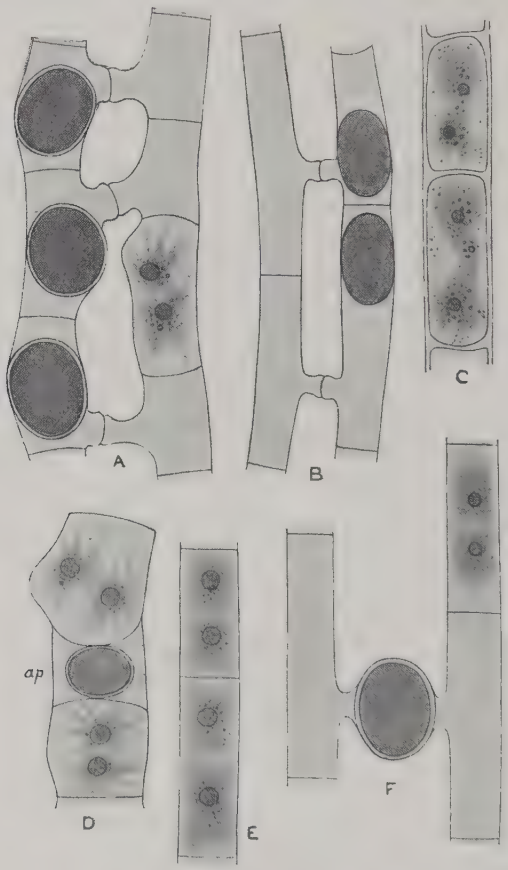

Fig. 97. A, *Zygnema stellinum* (Vauch.) Ag., from Cam Fell, W. Yorks (×430). B, Z. *Vaucherii* Ag. var. *stagnale* (Hass.) Kirchn., from near the Lizard, Cornwall (×430). C, *Zygogonium ericetorum* Kütz., from Rombald's Moor, W. Yorks (×415). D, Z. *leiosperum* De Bary, from Esher Common, Surrey (×430), a portion of a filament which was conjugating along the greater part of its length. E, Z. *insigne* (Hass.) Kütz., from Malham, W. Yorks (×330). F, Z. *Ralfsii* (Hass.) De Bary, from Chippenham Fen, Cambridgeshire (×430). *ap*, parthenospore.

Z. *peliosporum* Wittr., with blue-black zygosp. lodged in the inflated female cells, has been recorded by Puymaly[2] from terrestrial habitats.

[1] Often regarded as a variety of Z. *pectinatum*.

[2] C. R. Paris, CLXXV, 1922, p. 1229.

Spirogyra Link, 1820[1]. Filaments composed of cylindrical cells, very variable as regards their diam. and relative length, with firm walls and an outer mucous coat which renders the threads very slimy; septa mostly quite plane, but a number of the smaller sp. possess "replicate" end-walls (cf. p. 232 and fig. 98, C), a character which is constant for the sp., though the ingrowths are not necessarily present at the extremities of every

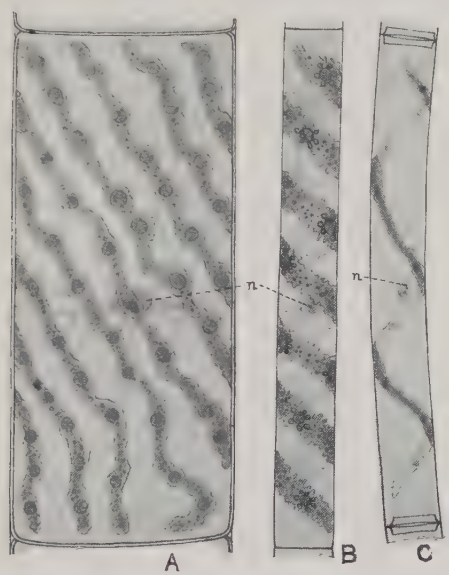

Fig. 98. A, *Spirogyra majuscula* Kütz., from Coates, Gloucestershire, single cell showing chloroplasts and nucleus (×300). B, *Spirogyra* sp., from the same locality (×370). C, *S. tenuissima* (Hass.) Kütz., from Mitcham Common, Surrey (×390). *n*, nucleus.

cell. Chloropl. parietal, in the form of spiral bands, usually from 1–7 per cell, sometimes very closely coiled, in other sp. (e.g. *S. majuscula* Kütz. (fig. 98, A)) practically straight and longit.; chloropl. either narrow with a smooth margin and a regular axile series of pyrens. (e.g. *S. neglecta* (Hass.) Kütz.) or broad with serrated margins and scattered pyrens. (e.g. *S. nitida* (Dillw.) Link, *S. porticalis* (Vauch.) Cleve) and between the two extremes there are all gradations. Kolkwitz[2] has shown

[1] De Bary, 1858, p. 1; Petit, *Sp.* d. env. d. Paris, 1880; Fritsch and Rich, Ann. of Bot. XXI, 1907, p. 423; Karsten, Flora, XCIX, 1908, p. 1; Tröndle, Zeitschr. f. Bot. III, 1911, p. 593; Cunningham, Bot. Gaz. LXVI, 1918, p. 272; Peterschilka, Arch. f. Protistenk. XLVI, 1923, p. 153; Czurda, ibid. LI, 1925, p. 439; Lloyd, Trans. Roy. Canadian Inst. XV, 1924, p. 129.

[2] Festschr. f. Schwendener, 1899, p. 271.

that the chloropl. grow in length in the direction of the coils by both apical and intercalary growth. Nucleus suspended in centre of cell, often clearly visible in living specimens, the protoplasmic strands linking it to the lining cytoplasm commonly reaching the latter exactly opp. a pyren. (fig. 98, A). Cell-sap often rich in tannins, and upon this depends the use of sp. of this genus for various permeability experiments.

Conjug. scalariform or lateral, zygosp. always in the female cell which frequently becomes considerably inflated. Mature zygosp. globular, ellipsoidal, cylindrical with obtuse ends, or more rarely flattened and discoid; the middle coat of the membrane often ornamented. *Re* hybrids, see p. 238.

There are about 25 Brit. sp. which for the most part have a distinct preference for low-lying quiet waters, such as those of ponds and ditches. They occur abundantly as bright green flocculent masses, often several feet in diam. Specific distinction is based on the character of the septa (whether replicate or not), the number of chloropl. and the number of turns of the spirals per cell, the form of the cells containing the zygosp. (whether inflated or not), the characters of the zygosp. themselves, and the dimensions of the threads; in all of these respects there is considerable constancy in the different sp. The smallest sp. is *S. gracilis* (Hass.) Kütz. (minimum br. about 10 μ) with plane septa, a single chloropl., and fructif. cells inflated only on the side adjacent to the conjugation-tube; the largest sp. is *S. crassa* Kütz. (max. diam. about 165) with 4–12 chloropl. per cell and broadly oval, somewhat flattened zygosp. Several sp., such as *S. tenuissima* (Hass.) Kütz. (fig. 98, C), *S. gracilis* (Hass.) Kütz., *S. communis* (Hass.) Kütz., *S. varians* (Hass.) Kütz., *S. affinis* (Hass.) Petit, and *S. nitida* (Dillw.) Link (fig. 94, A) are abundant in every part of the Brit. Isles except in the most mountainous districts. *S. tenuissima* and *S. affinis* are sp. frequently exhibiting lateral conjug. (cf. fig. 94, D). *S. velata* Nordst. (fig. 94, G) and *S. calospora* Cleve are notable for their beautifully marked zygosp.: those of the former have been observed to germinate immediately after their formation[1] without the development of a thick wall (fig. 94, E and F). A very remarkable sp. is *S. colligata* Hodgetts[2], with peculiar H-shaped pieces of membrane between adjacent cells and frequent conjug. between two cells by processes which grow through the septa. Sp. of *Spirogyra* are usually most prominently developed during the spring months when conjug. mostly occurs; some exhibit also an autumnal phase with an intervening period of scarcity or complete disappearance. The time of appearance of sp. of this genus in the spring depends upon the realisation of a certain concentration of the water[3], and

[1] West and West, 1898, t. V, figs. 84, 85.

[2] Hodgetts, Ann. of Bot. XXXIV, 1920, p. 519.

[3] cf. Fritsch and Rich, loc. cit. and 1913, p. 19 et seq.; Hodgetts, 1921, p. 17.

heavy autumnal and winter rainfall leads to a late occurrence. Sp. of *Spirogyra* often cause trouble in Cress-beds, the matted masses preventing the growth of the plants.

Family 3. MOUGEOTIACEAE

The members of this family are distinguished by the fact that the gametes become cut off from the gametangia by the development of special division-walls. This may take place either prior to (*Sirogonium*), during (*Zygogonium*), or subsequent to (*Mougeotia*) conjugation. Some part of the cytoplasm of the gametangia is unused in the conjugation-process. The zygospore is usually located in the canal, but in *Sirogonium* it lies in the female cell. In *Gonatonema* no conjugation occurs and the spores are cut off by two division-walls from the cells producing them.

Zygogonium Kützing, 1843 pro parte; emend. De Bary, 1858[1]. Filaments terrestr. or aquat., very occasionally branched, cell-wall often strongly thickened and stratified and cell-sap frequently purple or violet owing to phycoporphyrin[2]. Chloropl. single (splitting into two just prior to cell-division), axile, deeply constricted, sometimes twisted at the middle, with one pyren. in each of the irregular lobes (fig. 99, G). Gametes formed from greater part of cytoplasm of gametangia and cut off from the residue, after passing into the conjug.-process, by a curved wall (fig. 99, D); prior to fusion each gamete secretes a thin membrane around itself. Zygosp. subellipsoidal or subglobose, occupying the whole of the canal, with a several-layered envelope (fig. 99, E), the outer layer of which is formed from the special membranes secreted by the gametes before conjug. Azygosp. (parthenospores) also known.

In its present limits this genus includes only the sp. *Z. ericetorum* Kütz. (figs. 97, C; 99, D–G) which is a very widely distributed Brit. terrestr. Alga. It lives equally well in water, as on all kinds of peaty and sandy soil, being especially common on damp heaths or peaty moors. The frequent purple colour, due to phycoporphyrin in the sap, is usually not apparent in shaded situations, but rapidly develops on exposure to stronger light. The Alga possesses a great power of drought-resistance[3]: the dried mats are hard and horny, but absorb moisture almost instantaneously. According to G. S. West (1904, p. 129) this Alga fulfils an important function on some of the heaths and moors. "In the drier and hotter periods of the year thickly-

[1] De Bary, 1858, p. 79; West and Starkey, New Phytol. xiv, 1915, p. 194; Fritsch, Ann. of Bot. xxx, 1916, p. 135; Hodgetts, New Phytol. xvii, 1918, p. 238.

[2] Lagerheim, Vidensk. Selsk. Skrift. i, Mat.-nat. Kl., 1895, No. 5, p. 4.

[3] Fritsch, 1922; Fritsch and Haines, Ann. of Bot. xxxvii, 1923, p. 683.

matted sheets of *Z. ericetorum*, often many square feet in extent, are found covering wide patches of almost bare sand or peat, round such plants as *Drosera*, *Carices*, etc. These mats greedily take up water and in this way they regulate the moisture of the surface soil, the thriving of some of the smaller Phanerogams depending to a great extent on the presence of the Alga."

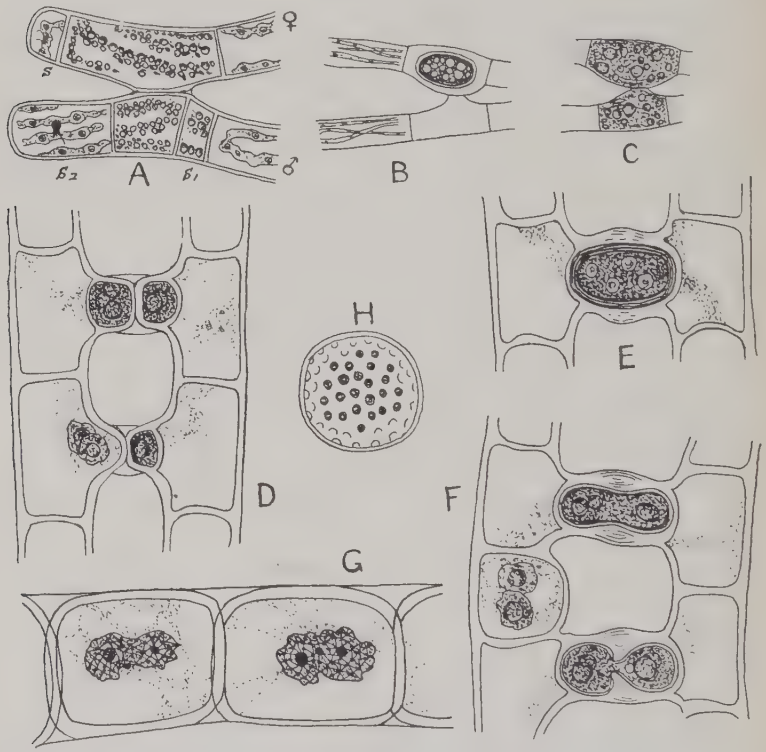

Fig. 99. A–C, *Sirogonium sticticum* Kütz.: A, showing the divisions preparatory to conjugation (after De Bary, ×125); *s*, s_1, etc., sterile cells; B and C, from Ingleton, W. Yorks (×90). D–F, *Zygogonium ericetorum* Kütz. (after Hodgetts, ×450), from Wyre Forest, Worcestershire; D and F, various stages in conjugation; E, zygospore. G, the same, vegetative cells (after West and Starkey, ×1200). H, *Zygnema stellinum* (Vauch.) Ag., zygospore (after Boergesen).

The cell-structure is often difficult to make out and some states of the Alga greatly resemble sp. of *Microspora* or *Rhizoclonium*. In dry situations the cells of the terrestr. form may have very thick walls and often harbour countless small fat-bodies, frequently arranged in a dense peripheral layer beneath the wall (cf. Fritsch). Conjug. has rarely been observed, but a detailed account of it was recently

published by Hodgetts based on material from Wyre Forest, and this account the present writer is able to confirm from his own observations on material repeatedly examined from Redlands Woods, Holmwood, Surrey.

Sirogonium Kützing, 1843[1] (*Choaspis* S. F. Gray, 1821)[2]. Filaments very similar to those of *Spirogyra*, although the cells contain more or less straight longit. chloropl.: there is a remarkable absence of the external mucous coat, in consequence of which this is the only member of Zygnemales which is not slimy or slippery. Conjug. only affects a few of the cells of each filament: no distinct tubes formed, the conjug. cells coming into contact by genuflexion (esp. of the female cells) and a perforation forming at the point of contact. Prior to conjug. the male gametangia are cut off by two and the female by a single div. (cf. p. 236): the resulting cells are of unequal size and (esp. the female) become somewhat swollen, the chloropl. completely disintegrating, even before contraction of the gametes occurs. Zygosp. in the female cell.

S. sticticum Kütz. (fig. 99, A–C), the only Brit. sp., has cells (40–50 br.: 2–6 times as long) containing several more or less longit. chloropl.; the zygosp. are ellipsoidal, about 75 × 42. The Alga usually occurs attached to stones over which the water is running fairly fast; it is also said to occur in stagnant water.

Mougeotia Agardh. 1824[3] (*Staurospermum* Kützing, 1843; *Mesocarpus* Hassall, 1845; *Craterospermum* Braun, 1855; *Plagiospermum* Cleve, 1868). Filaments composed of elongated cells, often narrow and with relatively thin walls, each with a thin axile plate-shaped chloropl. resembling that of *Debarya*. Chloropl. of adjacent cells usually in the same plane, so that a whole filament shows them in surface or in profile; rotation of the chloropl. from the surface to the profile position results on exposure to strong sunlight in about 30 minutes[4]. Nucleus apposed to one surface of the chloropl., in the middle of the cell (fig. 100, B). In the process of conjug. (nearly always scalariform) the greater part of the cytoplasm of the gametangia passes into the canal where fusion occurs; subsequently, and before the development of a membrane by the zygote, the latter becomes cut off from the gametangia by two (fig. 100, F), three, or four (fig. 100, I) walls; the number of surrounding sterile cells thus produced depends upon the position and size

[1] De Bary, 1858, p. 13. [2] cf. West, 1916 *a*, p. 353, footnote.
[3] De Bary, 1858, pp. 16, 19; Wittrock, Bih. K. Sv. Vet.-Akad. Handl. 1, No. 1, 1872, p. 35.
[4] Lewis, Ann. of Bot. XII, 1898, p. 418.

of the zygosp. and is subject to some variation in one and the same sp. Zygosp. spherical, or quadrate and more or less flattened with rounded or truncate angles; the outer layer of the membrane is formed by the conjug.-canal and the above-

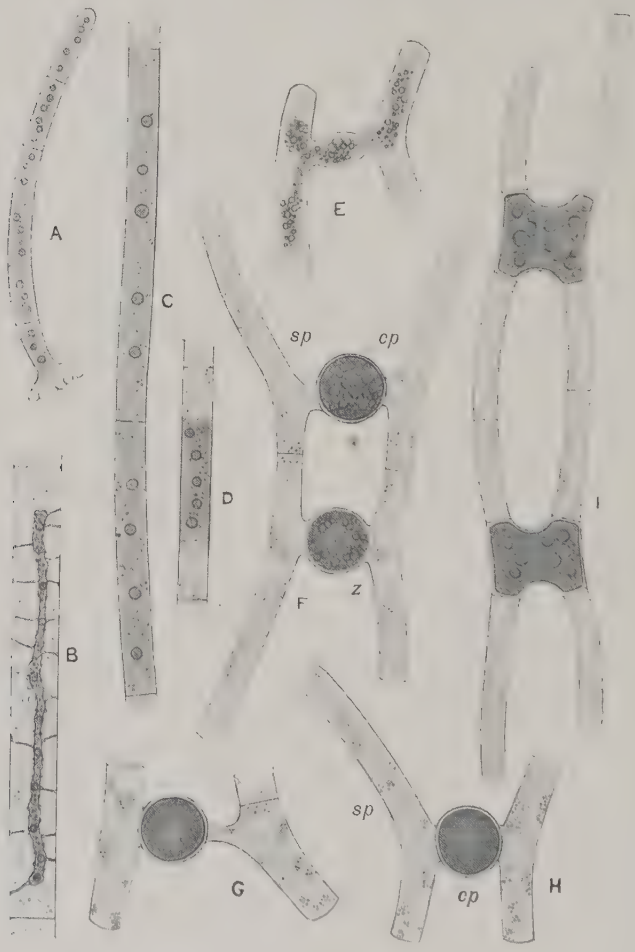

Fig. 100. A, *Mougeotia* sp., from Frizinghall, W. Yorks, young filament showing organ of attachment (×100). B, *M. capucina* (Bory) Ag., from the New Forest, Hants, showing edge of plate-like chloroplast (×430). C, *M. viridis* (Kütz.) Wittr. (×445). D–H, *M. parvula* Hass.; D–F, from Epping Forest, Essex; G and H, from near Settle, W. Yorks (×445). I, *M. gracillima* (Hass.) Wittr., from Esher West-end Common, Surrey (×445). *cp* and *z*, zygospore; *sp*, gametangium.

mentioned septa, further continuous thickening layers being deposited internally, while the surrounding sterile cells remain attached to the zygosp. for a long time.

As in other Zygnemales irregularities in conjug. are occasionally observed. The terminal cell of a thread sometimes enters into conjug. through its free end without the development of a tube. Conjug. has been recorded between cells of three distinct filaments, whilst in *M. capucina* double zygosp. (cf. certain Desmids, p. 261, and abnormal cases in *Spirogyra*, p. 237) have been noted. Conjug. between different sp. has rarely been recorded.

Sp. of this genus are extremely abundant in mountain tarns and lakes, and in the summer months they flourish in small pools up to 3000 ft. elevation. In such situations conjug. is rare and the Algae persist through the winter largely by the formation of resting akinetes, which are of the same form as the vegetative cells. In the plankton of large lakes the filaments are often much twisted and coiled (cf. West and West, 1905, p. 497; West and West, 1909 *a*, p. 169).

There are about 15 Brit. sp., of which *M. scalaris* Hass. (32–35 br.) is the largest and *M. elegantula* Wittr. (3·5–4·5 br.) is one of the smallest; the former has rounded and the latter quadrate zygospores. The two most abundant sp. are *M. parvula* Hass. (fig. 100, D–H) and *M. gracillima* (Hass.) Wittr. (fig. 100, I), which conjugate freely in all parts of the country and at all elevations up to 1200 ft. *M. genuflexa* (Dillw.) Ag., which often shows lateral conjug., is frequent in ditches and pools. *M. gelatinosa* Wittr. is one of the rarest Brit. sp.; it is characterised by a curious gelatinous investment of the zygosp. In *M. capucina* (Bory) Ag. the chloropl. sometimes assumes the form of an irregular axile rod, connected with the lining layer of cytoplasm by fine colourless strands, while the vacuoles contain a purple sap.

Gonatonema Wittrock, 1878[1]. Filaments similar in all respects to those of *Mougeotia*, but reprod. effected solely by parthenospores formed generally from the whole of the protoplasm of the cells, the latter usually becoming genuflexed at their point of formation. During the development of the spores, and just before the rounding off of the protoplast, the latter in rare cases divides more or less completely into two. The mature spores occupy only a small median portion of the cells producing them and are cut off from the empty parts by two septa; there is a greater difference in size between the spores of different sp. than can be accounted for by the difference in cubical capacity of the parent-cells.

[1] Wittrock, Bih. K. Sv. Vet.-Ak. Handl. v, 1878, No. 5; West and West, 1897, p. 476; West and West, 1898, p. 39; West and West, 1902, p. 17.

Sp. of this genus are amongst the rarest of the Conjugatae. *G. notabile* (Hass.) Wittr. (*Mesocarpus notabilis* Hass.), with cells 12–15 br., has not been found since its discovery by Hassall in 1845. *G. ventricosum* Wittr. (cells 7·5–8·6 br.) (fig. 101, G–J) is known from Ireland,

Fig. 101. A–F, *Gonatonema Boodlei* W. & G. S. West, from Mitcham Common, Surrey. G–J, *G. ventricosum* Wittr., from the river above Crolly Bridge, Donegal, Ireland. (All × 445.) *a*, parthenospore.

and *G. Boodlei* W. & G. S. West (cells 5–5·5 br.) (fig. 101, A–F) has been found in Surrey. The parthenospores of *G. ventricosum* differ considerably from those of *G. Boodlei* and are sometimes produced by the swelling of the free end of the terminal cell of a thread.

Series II. DESMIDIACEAE (Placoderm Desmids)

The Placoderm Desmids are remarkable for their great diversity of form, the often extraordinary complexity of the cell-outlines, and their wonderful symmetry. They include indeed some of the most beautiful of microscopic objects. The majority are unicellular, but a certain number of genera are colonial, the individuals being united in most cases to form long filaments (fig. 118). Desmids are essentially free-floating and frequently occur in great abundance in small ponds, in the quiet margins of rocky lakes, in *Sphagnum*-bogs, and in other favourable localities, but they are altogether restricted to freshwaters[1].

Except in *Closterium* (fig. 106) and some species of *Penium* the Desmid-cell exhibits a more or less distinct constriction into two perfectly symmetrical halves (fig. 103, C–F); each half is termed a *semicell* (even where no constriction occurs) and the narrower part connecting the two semicells is known as the *isthmus*. The excavation resulting on either side from the constriction or narrowing of the cell is known as the *sinus* and in most deeply constricted forms this is linear (fig. 103, F).

There are several thousand known species of Desmids about one-sixth of which are British, and almost all of them can be readily identified by their external morphological features. Some are cylindrical with rounded (e.g. *Penium* (fig. 105, A–C)), truncate (e.g. *Pleurotaenium* (fig. 108)), or attenuated (e.g. *Closterium* (fig. 106)) apices. Many of them are flattened, as is the case with most species of *Cosmarium* (fig. 112) and all species of *Euastrum* (fig. 110), whilst in *Micrasterias* (fig. 111) the majority of the species are disciform. In such flattened Desmids there are three principal planes of symmetry at right angles to one another and they require to be examined in three positions. The most important aspect is the *front-view* (fig. 103, F, *f*), in which the cell is observed in the plane containing the two longest axes and in which it naturally rests. The other important aspects are the *vertical-* or *end-view* (fig. 103, F, *v*) and the *side-* or *lateral-view* (fig. 103, F, *s*). In the genus *Staurastrum* (fig. 103, E; fig. 115) the cells have a radiate character, with 2-, 3-, 4-, or more-angled end-views, the corners being often drawn out into long processes.

The wall of the Desmid-cell invariably consists of two halves[2],

[1] *Cosmarium salinum* Hansg. has been described as inhabiting brackish water (cf. Hansgirg, Österr. Bot. Zeitschr. xxxvi, 1886, p. 335).

[2] Of more than two pieces in a few species of *Closterium* (p. 270) and *Penium* (p. 268).

one of these belonging to an older generation than the other. The two halves have bevelled edges and fit so closely over one another and are so firmly connected that they are not easily recognisable in the living individual, especially not in many of the constricted forms. They come apart, however, during conjugation (cf. fig. 104) and sometimes after death; separation can often also be induced by treatment with alkalis. The mature wall is further composed of two well-differentiated layers. The inner one is structureless and consists mainly of cellulose; the outer is stronger and thicker and is composed of a basis of

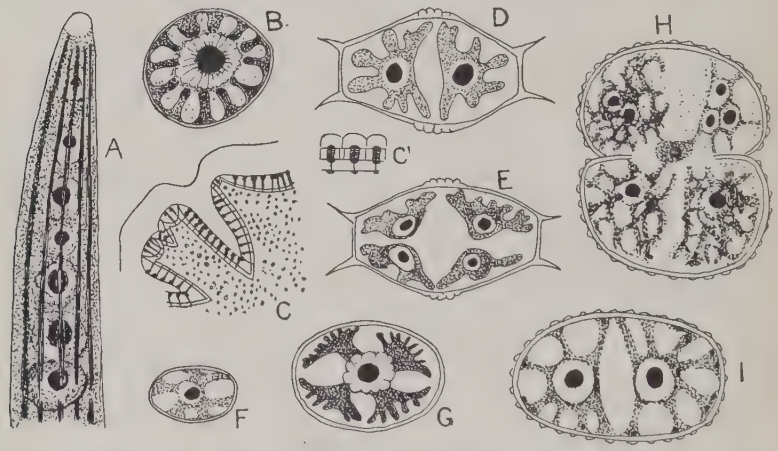

Fig. 102. A–B, *Closterium lanceolatum* Kütz. (after Carter); A ×350; B, transverse section ×550. C, *Micrasterias Crux-melitensis* (Ehrenb.) Hass., small part of cell, stained with methylene blue (after Schröder, ×440). C′, *Cosmarium turgidum*, pore-organs (after Hauptfleisch). D–E, *Xanthidium Brebissonii* Ralfs (after Carter, ×350), transverse sections of two different individuals. F, *Cosmarium subtumidum* Nordst., and G, *C. pseudopyramidatum* Lund., transverse sections (after Carter, ×550). H–I, *C. reniforme* (Ralfs) Arch. (after Carter, ×550).

cellulose impregnated with various other substances which include iron-compounds (most prominent in some species of *Closterium* and *Penium*). This outer layer frequently bears granules, spines, warts, or other protuberances, most of which show a definite arrangement (cf. figs. 112, 113). External to it is a thin diffluent mucilaginous coat (fig. 102, C), but in some Desmids the mucus is more abundant, completely surrounding the individual or, in colonial forms, the colony. This mucilage is frequently the home of epiphytes or of numerous rod-shaped Bacteria. It is by means of the mucous envelope that Desmids adhere to other larger aquatic plants and sometimes, when

rapid multiplication has taken place, enormous numbers of individuals occur embedded in masses of jelly. Sometimes the mucus is very tough, as for instance when it forms the pads or processes by means of which the individuals are connected in the filamentous forms (figs. 116, 117). The cell-wall sometimes contains a trace of silica.

The mucilage is secreted through pores[1] which traverse the wall (fig. 102, C) and are not uncommonly clearly recognisable without special treatment; they are absent in *Penium* and some small species of *Cosmarium*. In several genera the pores are almost uniformly distributed (e.g. *Micrasterias* (fig. 102, C)), except that they always appear to be lacking in the region of the isthmus. In richly ornamented forms, like many of the species of *Cosmarium*, they are commonly grouped symmetrically around the bases of the spines, warts, etc. of the outer layer of the wall. In *Closterium* they are arranged in longitudinal rows in the narrow grooves between the fine ridges with which the membrane is here often provided.

In the inner layer of the wall the pore[2] is a simple canal, but in the outer the canal is surrounded (in all genera except *Closterium*) by a specially differentiated cylindrical zone, not composed of cellulose. This is termed a "pore-organ" (fig. 102, C′) by Lütkemüller who has investigated these structures most fully. The canals are no doubt in all cases occupied by threads of mucilage in process of excretion. At the inner surface of the wall they often terminate in lens- or button-shaped swellings, whilst from the outer end of the pore-organs there sometimes arises a delicate radiating or club-shaped mass of mucilage through which the canal passes and which apparently may be more or less permanent in character (fig. 102, C′); mostly, however, these external processes are altogether wanting or merely represented as small perforated buttons (fig. 102, C). In many of the larger Desmids there are numerous smaller thread-like pores between the bigger ones and confined to the outer layer of the wall.

The envelope of mucilage which, as Schröder has shown, can usually be readily demonstrated by placing the cells in diluted Indian ink, for which the mucus has no affinity, often (except *Closterium*, *Arthrodesmus*) exhibits a prismatic or fibrillar

[1] Klebs, Unters. Bot. Inst. Tübingen, II, 1886, p. 378; Hauptfleisch, Zellmembr. u. Hüllgallerte d. Desmidiaceen, Diss. Greifswald, 1888; Lütkemüller, Österr. Bot. Zeitschr. XLIV, 1894, p. 11, and Cohn's Beitr. z. Biol. d. Pfl. VIII, 1902, p. 347; Schröder, Verhandl. Nat.-med. Ver. Heidelberg, VII, 1902, p. 153.

[2] The structure is well seen on staining with concentrated fuchsin, gentian violet, etc. (cf. Schröder, loc. cit. p. 166).

structure, especially in the inner region. This structure no doubt corresponds to the exudation of mucilage through the individual pores in the form of a number of closely apposed prisms. Where special mucilage-masses are recognisable external to the pore-organs, each of these occupies the middle of one of the prisms.

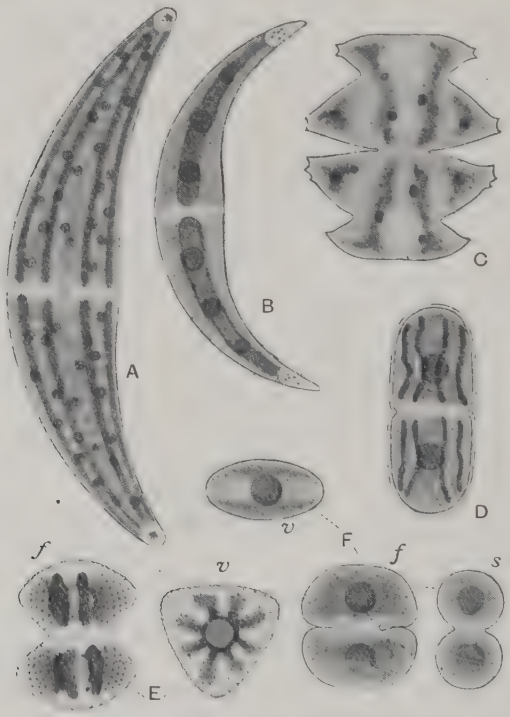

Fig. 103. A, *Closterium Ehrenbergii* Menegh., from Glyder Fawr, N. Wales (×184). B, *C. Leibleinii* Kütz., from near March, Cambs (×334). C, *Micrasterias oscitans* Ralfs var. *mucronata* (Dixon) Wille, from Kerry, Ireland (×184). D, *Cosmarium cucurbitinum* (Biss.) Lütk., from near St Just, Cornwall (×435). E, *Staurastrum Kjellmani* Wille, from 2600 ft. on Glyder Fawr, N. Wales (×435). F, *Cosmarium subtumidum* Nordst. var. *Klebsii* (Gutw.) W. & G. S. West (a form), from near Ely, Cambs (×435). *f*, front-view; *s*, side-view; *v*, end-view.

The slow movements frequently exhibited by Desmids, when in contact with a substratum, are due to local exudation of mucilage[1]. The latter is usually excreted through specially large pores situated near the ends of the cells, and irregular worm-shaped masses two or three times the length of the cell may be

[1] Klebs, Biol. Centralbl. v, 1885, p. 353; and Schröder, loc. cit. p. 158.

secreted at these points in the space of an hour. In *Closterium* the cells often perform pendulum-like movements about one fixed extremity; sometimes the free end swings through 180° to become attached in its turn, whilst the other repeats the movement. Thus, by a series of somersaults, each occupying 6–35 minutes according to the temperature, the cell moves forward over the substratum. In other genera the movements seem more erratic, although a forward gliding is sometimes noted.

The Desmid-cell always has a single nucleus which is usually embedded in a small median mass of cytoplasm (figs. 102, A, H; 103, A) in the region of the isthmus. The chloroplasts have recently been very thoroughly investigated by Dr Nellie Carter[1]. In the vast majority of cases they are axile and there is one in each semicell (fig. 102, F, G), although two occur in each semicell in many species of *Cosmarium* (fig. 102, H, I) and *Xanthidium* (fig. 102, D), as well as in *Euastrum verrucosum*. Such axile chloroplasts typically consist of a central portion (a rod in such elongate forms as *Closterium* (figs. 102, B and 103, B), and *Penium*; a central mass in other genera, cf. fig. 103, E), from which a number of plates or processes extend towards the periphery. There is a clearly recognisable tendency in many, and especially the larger, species of *Cosmarium*, *Euastrum*, etc. for the ends of these processes to spread out into parietal, sometimes richly lobed or fringed, plates within the bounding cytoplasmic layer (fig. 102, G), and the extent of this parietal development may vary considerably in one and the same species. In *Cosmarium Brebissonii* Menegh. some individuals have elaborate axile chloroplasts, whilst others have no axile system at all and instead possess a number of parietal chloroplasts (cf. also fig. 102, D and E). In several species (e.g. *Cosmarium Cucumis* Corda, *C. ovale* Ralfs, *Staurastrum tumidum* Bréb., many sp. of *Xanthidium* and *Pleurotaenium*) the chloroplasts are solely parietal and occur as a number of bands in each semicell. All the evidence points to a close relation between the two types of chloroplast-construction, the parietal system being probably a later development than the axile one and apparently often arising *pari passu* with an increase in the size of the cell.

In Desmids having axile chloroplasts the pyrenoids are usually located in the central portion (figs. 102, A, D, F, G; 103, B, D–F); in *Closterium* (fig. 103, B) and *Tetmemorus* there is a row of pyrenoids, in other cases a single one. Carter and Ducellier[2] have however drawn attention to the frequent multiplication of the central pyrenoid (cf. fig. 102, H), although since the

[1] Ann. of Bot. XXXIII, 1919, pp. 215, 295, and XXXIV, 1920, pp. 265, 303.
[2] Bull. Soc. Bot. Genève, 2 sér. IX, 1917, p. 3.

products of its division remain close together this may be difficult to recognise except in carefully fixed and stained specimens. This multiplication probably shows the way in which the scattered pyrenoids found in the chloroplasts of some forms have arisen; this condition is met with in *Closterium Ehrenbergii* (fig. 103, A), many species of *Euastrum*, and occasional species of *Cosmarium* (e.g. *C. Ralfsii* Bréb.) and *Staurastrum* (e.g. *S. grande* Bulnh.). A number of pyrenoids are also found in each of the parietal chloroplasts above mentioned. Carter[1] further records, in a considerable number of the species examined by her, small naked pyrenoids devoid of a starch-sheath, and such may be met with in the peripheral processes when the ordinary pyrenoids are restricted to the central mass.

In Desmids with large axile chloroplasts vacuoles may be absent or much reduced, but in those with parietal chromatophores large vacuoles are often present in the central parts of the cell. In *Closterium* (fig. 103, A and B) and *Pleurotaenium* there is a well-marked terminal vacuole at each extremity of the cell, containing one or many vibrating granules of irregular or definite shape; in *Closterium* they have been shown to be minute crystals of gypsum[2]. Their movements cease with the death of the cell. Circulation of the cytoplasm is often well seen in the larger species of *Closterium*, etc.

The usual method of multiplication is by cell-division, and in many species this would appear to take place indefinitely without conjugation occurring. It is a striking fact that in many frequently found Desmids sexual reproduction has either never been observed or only very rarely. On the other hand, in some species conjugating individuals are very commonly encountered. The process of cell-division is complicated by the bipartite structure of the wall and some points relating to it still remain obscure. Division occupies about a day in the smaller, several days in the larger species.

In a simple unconstricted form like *Hyalotheca* (fig. 118) the process shows much resemblance to that found in species of *Microspora*, division being initiated by the development of a cylindrical strip of membrane on the inner side of the wall at the level of the junction of the two semicells; the septum arises

[1] loc. cit. 1919, p. 226.

[2] If Desmids are kept in small glass vessels (i.e. under abnormal conditions) large vacuoles, generally containing numbers of minute pale yellow moving corpuscles different in appearance from those of *Closterium*, are found in the cytoplasm. When present in large numbers, they make the cell appear almost black. Under abnormal conditions they develop in most of the genera and at the same time the sap often acquires a violet colour owing to the appearance of phycoporphyrin.

from this as an annular ingrowth and later splits into two[1]. In Desmids with a marked median constriction (e.g. *Cosmarium*) the first step is an elongation of the isthmus, causing a slight separation of the two semicells and accompanied by the development of a cylindrical strip of membrane between them. The mode of origin of the strip of membrane is not altogether clear. Within the elongated isthmus a transverse septum is formed demarcating the two new halves and later splitting into two. The young semicells gradually enlarge, but usually remain in contact by their apices (fig. 112, L) until they are practically fully grown[2]. It would seem that in some cases the membrane of the new semicell remains smooth and that a second membrane with the typical ornamentation of the species develops on its inner side[3], but it is not known whether this is the rule or the exception. The cell-division of *Closterium* is of a rather different type and is dealt with on p. 269.

The young semicells are clearly recognisable and nuclear division is complete before any change takes place in the chloroplasts of the parent. At a certain stage, however, the choroplasts commence rapidly to enlarge and extend through the isthmus from the old into the new semicell, so that as the latter reaches its full size it is generally uniformly green. Division of the chloroplasts then occurs at the isthmus.

In the process of conjugation two[4] individuals become approximated and enveloped in mucilage; in the Cosmarieae they are not uncommonly placed at right angles to one another (fig. 104). In many Desmids the semicells of each individual come apart at the isthmus and the protoplasts are set free and fuse; in some cases, however, more or less distinct protuberances of variable size arise from the isthmus of each conjugating cell (fig. 104, B) and join to form a tube within which fusion occurs. In the filamentous types dissociation into the individual cells (figs. 118, H; 119, G) occurs prior to conjugation, except in certain species of *Desmidium* (e.g. *D. Swartzii*). The zygospore is formed between the conjugating cells with the sole exception of *Desmidium cylindricum* Grev.[5], where it is lodged within the

[1] This account is according to Hauptfleisch, loc. cit. p. 46. Acton (Ann. of Bot. xxx, 1916, p. 379) makes no detailed statements on this matter, nor do her figures show this mode of origin of the septum.

[2] cf. De Bary, 1858, p. 43; Lütkemüller, loc. cit. 1902, p. 360; Carter, loc. cit. 1920, Pl. XVI, figs. 61–65.

[3] Hauptfleisch, loc. cit. pp. 52, 53; Lütkemüller, p. 362.

[4] As an abnormality three or even four individuals may participate in the formation of a zygospore.

[5] Occasionally also in *Hyalotheca dissiliens* (cf. Boldt, Bih. Sv. Vet.-Ak. Handl. XIII, Afd. III, 1888, No. 5, t. II, fig. 53; Joshua, Journ. of Bot. xx, 1882, p. 301).

female cell (fig. 119, C). The mature zygospores have a membrane of three layers, of which the inner is thin and colourless, the middle one brown and firm, and the outer either smooth or covered with variously arranged warts or spines.

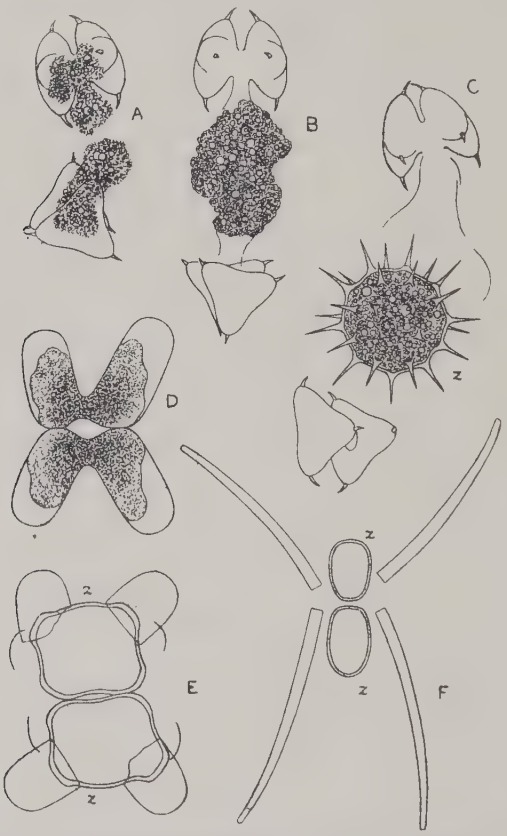

Fig. 104. A–C, *Staurastrum Dickiei* Ralfs; three stages in conjugation, from the New Forest, Hants (×356). D and E, *Penium didymocarpum* Lund.; D, conjugation of four individuals just produced by division; E, completed conjugation showing the double zygospore; from near Balallan, Lewis, Outer Hebrides (×464). F, *Closterium lineatum* Ehrenb., showing the double zygospore, from near Glenties, Donegal, Ireland (×100). *z*, zygospore.

It frequently happens that conjugation ensues between the two daughter-individuals immediately after division and before the young semicells have arrived at maturity[1]; in such cases

[1] Archer, Quart. Journ. Microscop. Sci. II, 1862, p. 251; W. and G. S. West, Journ. Roy. Microscop. Soc., 1896, p. 151.

there can be no question of marked differentiation of sex. Conjugation between adjacent cells of filamentous forms (i.e. lateral conjugation) has been observed in species of *Sphaerozosma* and *Spondylosium*, but such cases are very rare. It is unlikely that hybridisation will often occur in view of the rarity of conjugation in Desmids; in fact only one example has been described and this was not followed up[1].

Double zygospores (cf. *Spirotaenia*, p. 227) are formed as an occasional phenomenon in a number of species, but their production is the rule in *Closterium lineatum* (fig. 104, F), *C. Ralfsii* var. *hybridum*, *Cosmarium diplosporum*, and *Penium didymocarpum* (fig. 104, D and E). In the last-named species the paired zygospores are formed by conjugation between four cells produced by two consecutive divisions of one individual. In the two species of *Closterium* each zygospore is formed by the union of a pair of gametes, one produced from a semicell of each individual.

The formation of what are probably to be regarded as parthenospores has been observed very occasionally in species of *Closterium* and *Cosmarium*, as well as in *Spondylosium nitens* (Wall.) Arch.[2] and species of *Hyalotheca* (fig. 118, E)[3]. Klebs was also able to induce their formation artificially in *Closterium Lunula* and *Cosmarium Botrytis*[4].

The zygospores undergo a prolonged resting period and fusion of the gamete nuclei is delayed until just prior to germination, the details of which are only known in a few cases[5]. The chloroplasts of the gametes usually become indistinct during conjugation, but in the mature zygospores two chlorophyll-containing masses are often recognisable. According to Kauffmann[6] two of the four chloroplasts of the gametes disintegrate during maturation of the zygospores of *Penium*, *Closterium*, and *Staurastrum*. As in other Conjugatae, two successive nuclear divisions take place in the germinating zygospore; of these the first is presumably the reduction division. Thereupon the contents, which have escaped from the outer envelopes of the spore, divide into two individuals, each with one chloroplast and two nuclei, one of which enlarges while the other gradually

[1] Archer, Quart. Journ. Microscop. Sci. xv, 1875, p. 414. This was a zygospore produced by the conjugation of a cell of *Euastrum Didelta* with one of *E. humerosum*.

[2] Wallich, Ann. Mag. Nat. Hist., ser. 3, v, 1860, t. VII, fig. 14; Turner, K. Sv. Vet.-Ak. Handl. xxv, 1892, No. 5, t. XVIII, fig. 7.

[3] West and West, 1898, t. IV, figs. 23–27. [4] Klebs, 1896, p. 260.

[5] De Bary, 1858, p. 52; Millardet, Mém. Soc. sci. nat. Strasbourg, vi, 1870, p. 38; Klebahn, Jahrb. Wiss. Bot. xxii, 1890, p. 420.

[6] Zeitschr. f. Bot. vi, 1914, p. 764.

disappears. The production of two individuals would seem to be usual in Desmids, but in some cases there are four[1]. The first-formed cells are devoid of the characteristic markings of the species, but these are acquired by the new semicells after the first vegetative division.

The phylogeny of the Desmidiaceae is a debatable matter. G. S. West[2] regarded them as "a degenerate family of Conjugatae which has originated by retrogression from filamentous ancestors. The degeneration has brought about a loss of the filamentous condition, accompanied by the development of specialised morphological characters, and this has gone hand in hand with the loss of sexual differentiation of the conjugating cells" (West, 1904, p. 142). *Debarya Desmidioides* W. & G. S. West was regarded as filling "up the link that was missing in the chain of evidence which goes to show that *Cylindrocystis* and *Mesotaenium*, and following on that nearly all the other genera of Desmids, were most probably derived from filamentous ancestors" (p. 143). It is impossible to gainsay the possibility of such a view being correct, since degeneracy of the Desmids is perhaps also shown in the rare occurrence of conjugation in many species. At the same time there are many difficulties to face if one adopts this view, not the least of which is the mode of origin of the elaborate wall-structure of the Placoderm Desmid.

The same difficulty is encountered in accepting Oltmanns' view that Zygnemales and Desmidiaceae have diverged from an ancestry resembling the Mesotaeniales (cf. p. 225); but it is the only difficulty. The Mesotaeniales present us in the main with simple forms possessing chloroplasts of a pattern like those of the other two series and four individuals are normally produced from the zygospore by contrast with the two of Desmidiaceae and the single one of Zygnemales. The fact that some Mesotaeniales produce only two, whilst Desmidiaceae may occasionally form four, does not in any way detract from the obvious primitiveness in this respect of the former. G. S. West also places *Cylindrocystis* and *Mesotaenium* at the base of his evolutionary scheme of Desmids, and the two views really only differ in the place assigned to the Zygnemales. The present writer altogether agrees with Oltmanns in placing Mesotaeniales first and Zygnemales as a probable elaboration of such forms. With regard to the Desmidiaceae proper, while recognising the great resemblance, it seems better to adopt a more conservative attitude, in view of the importance of a bipartite structure of the

[1] cf. Turner, Proc. Linn. Soc. London, 1922, p. 59.

[2] West and West, 1898, pp. 53, 55; G. S. West, Journ. Linn. Soc., Bot. XXXIV, 1899, p. 409; West, 1916 *a*, p. 377.

wall in other classes of Protophyta and its occasional occurrence also in some of the other groups of Isokontae.

There is undoubtedly a great tendency towards the secondary assumption of a filamentous condition in Desmids. Not only has this resulted in the production of true filamentous types (*Spondylosium*, *Desmidium*, etc.), but the same trend reveals itself in certain species of genera which are normally unicellular. Thus, filamentous forms are occasionally met with in species of *Cosmarium* (e.g. *C. obliquum* Nordst., *C. moniliforme* (Turp.) Ralfs, etc.), in *Euastrum binale* (Turp.) Ehrenb., and *Staurastrum inconspicuum* Nordst., whilst the tropical *Micrasterias foliacea* Bail. is a true filamentous member of a typically unicellular genus with complex cell-outlines.

Desmids, like other Algae, are subject to some variation, but the shape of the cell, the structure of the cell-contents, and especially the markings embellishing the exterior of the cell-wall, are often astonishingly constant[1]. No one who has seen Desmid-gatherings from different quarters of the globe can fail to be struck with the constancy of these characters. The outward form of the cell, as seen in front-view, varies within certain usually narrow limits, the shape of the end-view being generally more constant than that of the front-view. Prolific growth and rapid division have a tendency to produce variations from the typical form and such are usually found in the unnatural conditions of pure cultures[2]. On the other hand, changes in the conditions of the environment cannot affect the characters of a species, unless they act for a long period.

G. S. West (1904, p. 144) regarded it as highly probable that the complexity of outline of the Desmid, which is so frequently accompanied by a defensive armour of spines and processes, serves as a means of defence against the attacks of small aquatic animals. It is noticeable that species occurring on wet rocks and in other localities where Amoebae, Oligochaetes, Tardigrades, Crustacea, etc. are either absent or very scanty, especially at high elevations, usually possess a comparatively simple outline and are provided with more or less abundant mucilage; whereas species occurring in deep bog-pools, in the plankton, and the quiet margins of deep lakes, in which localities such enemies abound, are generally possessed of a more complicated, and in many cases of a formidable exterior. Many species of plankton-

[1] De Wildeman, Annales Soc. Belge de Microscop. XVIII, 1894, p. 57; G. S. West, loc. cit. p. 376; Comère, Bull. Soc. Bot. France, LIV, 1907, p. xlii; Ducellier, Bull. Soc. Bot. Genève, VII, 1915, p. 75.

[2] With reference to such cultures, see Pringsheim, Ber. Deutsch. Bot. Ges. XXXVI, 1918, p. 482.

Desmids are highly adapted to a floating life, either by the possession of a thin plate- (*Micrasterias*) or needle-like form (some sp. of *Closterium*), by the protrusion of the cell into more or less elongated processes (*Staurastrum*), or the presence of long spines (*Xanthidium*, *Arthrodesmus*); such equipment no doubt also constitutes a mechanism for anchorage in times of flood.

The only area from which Desmids are seemingly practically absent is the Antarctic continent. As our knowledge of the geographical distribution of members of this family increases, it is becoming apparent that they are by no means ubiquitous, as has often been supposed. True, a considerable number of species seem to enjoy a practically world-wide distribution. There are many species, long since described and easily recognisable, however, which have only been recorded from certain parts of the world, and G. S. West was among the first to draw attention to what seem to be definite American, Arctic, African, etc. types. Since Desmids so rarely form zygospores, dispersal over any great area is probably a slow process; the ordinary individuals are very sensitive even to partial drying, and submergence in sea-water is equally fatal. Under these circumstances carriage over any wide expanse of sea by birds is out of the question, except for very small species or for the rarely formed zygospores. Dispersal has probably in the main been effected over land-surfaces by slow steps from piece of water to piece of water, and it is therefore not out of the question that a sound knowledge of the distribution of Desmids would shed much light on the subject of previous land-connections.

Within a limited area such as the British Isles the distribution of Desmids seems largely conditioned by ecological factors. Desmids thrive best in soft water and they are usually most numerous in peaty water which has a trace of acidity. With few exceptions (e.g. *Cosmarium Dovrense*, *Oocardium stratum*) they do not flourish in water containing carbonate of lime in solution. Certain Desmids are habitually found on wet dripping rocks among Bryophytes (e.g. *Cosmarium anceps*, *C. Holmiense*, *C. pseudarctoum*, *Staurastrum Meriani*, etc.). Others may be described as montane being found only at higher altitudes (e.g. *Cosmarium cymatopleurum*, *C. cyclicum*, *Staurastrum acarides*, *S. Kjellmani*, etc.)[1]. Messrs West[2] have further shown that in the British Islands one can distinguish a western Desmid-flora restricted to pieces of water combining a suitable habitat with drainage-water derived from geological formations older than the Carboniferous; this includes such distinctive forms as

[1] W. and G. S. West, Monogr. Brit. Desm., Ray Soc. 1, 1904, p. 14.
[2] West and West, 1909 *a*, p. 199.

Staurastrum Ophiura, *S. Cerastes*, *S. Arctiscon*, *Micrasterias radiata*, *Pleurotaenium nodosum*, etc. Many of the larger British lakes possess a plankton in which such Desmids play an important rôle[1], and Pearsall[2] has shown that such are characterised by a rocky basin, and waters with a high ratio of sodium and potassium, as compared with calcium and magnesium.

Especially typical of ponds are various species of *Closterium* (e.g. *C. moniliferum*, *C. acerosum*, *C. rostratum*, etc.), *Cosmarium Botrytis*, *C. granatum*, *C. Meneghinii*, and *Staurastrum punctulatum*.

The classification of Desmids is not altogether easy. Whereas the genera are readily distinguished from one another as far as the bulk of their species is concerned, a certain number of the latter are usually difficult to assign, since at their limits the genera pass over into one another. In no other group of Algae can such complete sets of transitional forms be found. Our knowledge of British Desmids has been very materially advanced by the excellent monograph of W. and G. S. West[3], which has been of fundamental importance for the study of the group.

The following synopsis, which also includes the Saccoderm Desmids (cf. p. 225), is reproduced with little modification from that given in the earlier edition of this work:

I. Cell-wall unsegmented and without pores, point of div. of cells indefinite[4] *Saccoderm Desmids* (*Mesotaeniales*, p. 225)

A. Cells not many times longer than broad

a. One chloropl. in each cell

1. Chloropl. spirally twisted, axile or parietal *Spirotaenia* (p. 227)

2. Chloropl. plate-shaped, axile *Mesotaenium* (p. 229)

b. Two chloropl. in each cell

1. Chloropl. stellate with a large central pyren. *Cylindrocystis* (p. 229)

2. Chloropl. with a central rod bearing longit. ridges *Netrium* (p. 230)

B. Cells usually many times as long as broad[4] *Roya* (p. 230)

II. Cell-wall segmented, with a differentiated outer layer, and usually with pores, cell-div. follows a fixed type, with the interpolation of younger halves between the old ones *Placoderm Desmids* (p. 253)

[1] cf. also Pearsall and Pearsall, Journ. Linn. Soc., Bot. XLVII, 1925, p. 55.

[2] Proc. Roy. Soc., B, XCII, 1921, p. 276; and Rev. algol. I, 1924, p. 53.

[3] Ray Society, vols. I–V, 1904–1923. The last volume with the collaboration of Dr N. Carter.

[4] cf. also Gonatozygaceae, p. 240.

A. Point of div. of cells variable or sometimes fixed (at the isthmus)
  a. Cells short or of moderate length, straight, cylindrical, sometimes with a slight median constriction: wall without pores: point of div. of cell sometimes variable; girdle-bands (p. 270) commonly present *Penieae*
    Only genus *Penium*
  b. Cells elongate, generally curved and attenuated towards each extremity; wall usually with pores, often longit. striated: point of div. in middle region of cell: girdle-bands present in some sp.; apical vacs. with gypsum-cryst. *Closterieae*
    Only genus *Closterium*

B. Point of div. of cells always fixed (at the isthmus); cell-form very varied, but usually with a median constriction: wall of two thin firm layers traversed by pores; girdle-bands never formed *Cosmarieae*
  a. The septum formed during division of the cell remains plane
    1. Cells usually solitary, separating after div.
      * Cells elongated and cylindrical, constriction slight
        † Apices of cells truncate or rounded
          § Base of semicells plicate *Docidium*
          §§ Base of semicells plane *Pleurotaenium*
        †† Apices of cells cleft, incision open or narrow
          § Wall adorned with rings of furcate processes *Triploceras*[1]
          §§ Wall plane
            ‡ Apical incision widely open, each apical angle with a spine *Icthyocercus*[1]
            ‡‡ Apical incision narrow *Tetmemorus*
      ** Cells relatively short, end-view commonly elliptical or radiating, constriction usually deep
        † Cells compressed (at right angles to plane of front-view): end-view usually fusiform or elliptical
          § Cells generally with an apical incision and a central protuberance, moderately lobed *Euastrum*
          §§ Cells very compressed and deeply lobed or incised *Micrasterias*
          §§§ Cells with a more or less entire margin, often furnished with warts or spines
            ‡ Cells commonly with a central protuberance
              ⊙ Wall smooth, granulate, verrucose, etc.; central protuberance present or absent *Cosmarium*
              ⊙⊙ Wall with regularly arranged spines, commonly in pairs; central protuberance always present *Xanthidium*
            ‡‡ Cells without a central protuberance, angles spinate *Arthrodesmus*

[1] Not so far recorded in the British Isles.

†† End-view commonly radiating, triangular, 4-angular or up to 11-radiate, rarely fusiform *Staurastrum*

2. Cells attached to form colonies, not separating after div.

* Colonies spheroidal, cells not in contact, but joined by gelatinous bands

† Gelatinous bands narrow, microscopic colonies of few cells *Cosmocladium*

†† Gelatinous bands tubular, forked, calcified, macroscopic colonies of many cells *Oocardium*

** Colonies filamentous, cells attached by their apices

† Cells attached by special apical processes

§ Apical processes very short *Sphaerozosma*

§§ Apical processes long and overlapping the apices of the adjoining cells *Onychonema*

†† Apices of cells plane and flat

§ Cells deeply constricted

‡ End-view elliptical *Spondylosium*

‡‡ End-view 4-angular, with produced angles *Phymatodocis*[1]

§§ Cells very slightly constricted *Hyalotheca*

b. The septum formed during cell-division develops a girdle-like thickening or ingrowth, which projects both ways into each of the old semicells; cells attached to form filamentous colonies

1. Cells joined by special apical processes *Streptonema*[1]
2. Cells joined by their flat apices or by flattened apical projections

* Cells short, end-view fusiform, triangular, or 4-angular (rarely circular with produced angles) *Desmidium*

** Cells elongate, cylindrical *Gymnozyga*

Sub-family 1. Penieae

Penium Brébisson, 1844; emend. Lütkemüller, 1905[2]. Cells of moderate length, solitary, straight, cylindrical, subcylindrical, or ellipsoidal, with rounded or truncate apices, sometimes with a slight median constriction; vertical view always circular. Cell-wall without pores, sometimes quite smooth, but the inner layer often ornamented with striations, punctulations, or granulations; outer layer sometimes yellow or reddish-brown owing to iron-compounds. Chloropl. axile, one in each semicell, with radiating longit. plates with an entire margin; pyren. one, or several in a single series in the central body of the chloropl., in some sp. much elongated and surrounded by numerous starch-grains[3]. In some sp. the point of div. of the cell is variable

[1] Not so far recorded in the British Isles.

[2] Lütkemüller, Verh. Zool.-Bot. Ges. Wien, LV, 1905, p. 332.

[3] cf. Carter, loc. cit. 1919, p. 228.

and girdle-bands (see p. 270) may be formed as in *Closterium* (e.g. in *P. spirostriolatum* (fig. 105, C)). Zygosp. globose and smooth, more rarely subquadrate.

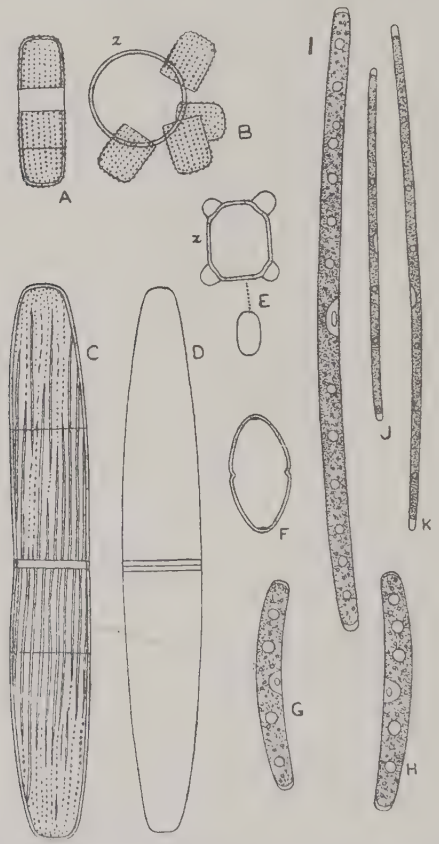

Fig. 105. A and B, *Penium Cylindrus* (Ehrenb.) Bréb.; A, from Loch Minnoch, Kirkcudbright; B, zygospore from Thursley Common, Surrey (×474). C, *P. spirostriolatum* Barker, from Kerry, Ireland (×474). D, *Closterium Libellula* Focke, from Bowness, Westmorland (×200). E, *Penium suboctangulare* West, with zygospore, from Killarney, Kerry, Ireland (×365). F, *Cosmarium curtum* (Bréb.) Ralfs, from Grimspound, Devonshire (×474). G and H, *Roya obtusa* (Bréb.) W. & G. S. West var. *montana* W. & G. S. West, from Baildon Moor, W. Yorks (×570). I, *R. Cambrica* W. & G. S. West, from Llyn Ogwen, N. Wales (×474). J and K, *R. Pseudoclosterium* (Roy) W. & G. S. West, from Pilmoor, N. Yorks (×474). *z*, zygospore.

Many sp. formerly included in this genus are now referred to *Netrium*, *Closterium*, or *Cosmarium*. There remain 16 Brit. sp. *P. mar-*

garitaceum (Ehrenb.) Bréb. and *P. Cylindrus* (Ehrenb.) Bréb. (fig. 105, A and B) are examples of granulated forms with reddish-brown walls, the former having a distinct median constriction. *P. spirostriolatum* Barker (23–26 br.; 123–274 l.) (fig. 105, C) is a sp. with girdle-bands and spiral striations, which often anastomose or become broken up into dot-like thickenings. *P. polymorphum* Perty (25–27 br.; 55–58 l.) is one of the most general of the upland, moorland sp. One of the smallest forms is *P. suboctangulare* West (6·8–7 br.; 10·7–11·5 l.) (fig. 105, E). *P. didymocarpum* Lund. develops double zygospores (fig. 104, D–E, and p. 261).

Sub-family 2. Closterieae

Closterium Nitzsch, 1817[1]. Cells solitary, elongate, without median constriction, generally distinctly curved, and often markedly lunate or arcuate, usually strongly attenuated towards the poles which are obtuse, truncate, rostrate, or drawn out into long needle-like points; cross-section circular (fig. 102, B). Cell-wall usually with pores, in many cases with delicate ridges running from pole to pole at regular intervals and appearing as striations whose number and strength vary much in different sp. Chloropl. axile, one in each semicell, composed of a central axis bearing a number of longit. ridges (fig. 102, A, B) which may be undulate or anastomosing; relative size of axis and ridges varies with the sp.; each chloropl. has one or several pyrens., usually arranged in a linear series in the axis. Extremities of chloropl. concave and not reaching the poles, where prominent apical vacs. containing one or many moving granules are located; in sp. in which the apices are greatly produced (e.g. *C. Kützingii*) the chloropl. do not extend into the prolongations and the apical vacs. are often correspondingly lengthened out.

The cell-division is peculiar and unlike that of other Desmids; it has been especially investigated by van Wisselingh[2] and Lütkemüller[3] whose conclusions are however at variance. A first peculiarity lies in the fact that the dividing wall is not formed at the boundary between the two semicells, but a little way beyond in the younger semicell; at this spot there arises a slight internal thickening of the wall and a slight external constriction ("Ringfurche") appearing superficially as a trans-

[1] De Bary, 1858, pp. 48, 54; Millardet, Mém. Soc. sci. nat. Strasbourg, VI, 1870, p. 38; Fischer, Bot. Zeit. XLI, 1883, p. 225; Klebahn, Jahrb. Wiss. Bot. XXII, 1891, p. 420; Lutman, Bot. Gaz. XLIX, 1910, p. 241, and LI, 1911, p. 401; Carter, loc. cit. 1919, p. 228.

[2] Zeitschr. f. Bot. IV, 1912, p. 337 and X, 1918, p. 629.

[3] Cohn's Beitr. z. Biol. d. Pfl. VIII, 1902, p. 372; and Ber. Deutsch. Bot. Ges. XXXV, 1917, p. 311, where a good summary of van Wisselingh's interpretation will be found.

verse line. When div. is about to take place, this local thickening becomes drawn out into a cylindrical strip owing to a slight elongation of the cell and from the strip a septum grows in as described on p. 258 for *Hyalotheca*[1]. It is at this point that the interpretations of the two above-mentioned investigators diverge. According to Lütkemüller the septum later splits and the two halves become bulged out to form the new semicells of the respective daughter-individuals. The one individual will thus possess a narrow connecting-band extending between the suture marking the connection between the two halves of the parent-cell and that marking the connection between the old and new semicells (cf. fig. 106, A). Each division will add a further connecting-band to the daughter-individual that acquires the older semicell. In this way the series of fine transverse lines to be seen in the equatorial region of many *Closteria* originate.

According to van Wisselingh, after formation of the septum, a complete layer of cellulose is deposited over the whole inner surface of the wall in each daughter-individual and, as the septum splits, this layer bulges out to form the new semicell. On his interpretation the wall of a *Closterium*-cell consists of one piece as far as the inner strata are concerned, but the older semicell will have several external strata overlapping one another and stopping short at various points, their limits marking the limits of the connecting-bands.

Girdle-bands are only developed in about a dozen of the Brit. sp. of *Closterium* (e.g. *C. intermedium* Ralfs. *C. striolatum* Ehrenb. (fig. 106, B–D), etc.) and there are never more than two of them. They arise by the development of an internal thickening of the wall in the younger semicell a little way from its point of junction with the older one; at this point the cell-membrane ruptures and the girdle is formed by stretching of the thickening ring between the ruptured portions (Lütkemüller) or by the stretching of a complete cellulose-layer apposed to the whole inner surface of the wall (van Wisselingh). The formation of a girdle is of course also accompanied by the production of an additional connecting-band.

Zygosp. commonly formed, generally globose and smooth (with conical papillae in *C. calosporum* Wittr.), but flattened and quadrate with truncate angles in certain sp. (e.g. *C. rostratum* Ehrenb. (fig. 106, G); *C. Kützingii* Bréb.).

There are 62 Brit. sp. which are distinguished by the size and shape of the cell, the structure of the wall, and the number of pyrens. in the chloropl. The curvature is often very constant, and in stating the

[1] It is not certain that these facts apply to all species of *Closterium*, only a small number having so far been investigated.

dimensions of a sp. it is usual to give, apart from the diam. across the middle, the distance between the apices and the curvature of the outer margin expressed in degrees of arc. The largest Brit. sp. is *C. turgidum* Ehrenb. (43–80 br.: 476–940 l.), whilst the smallest is

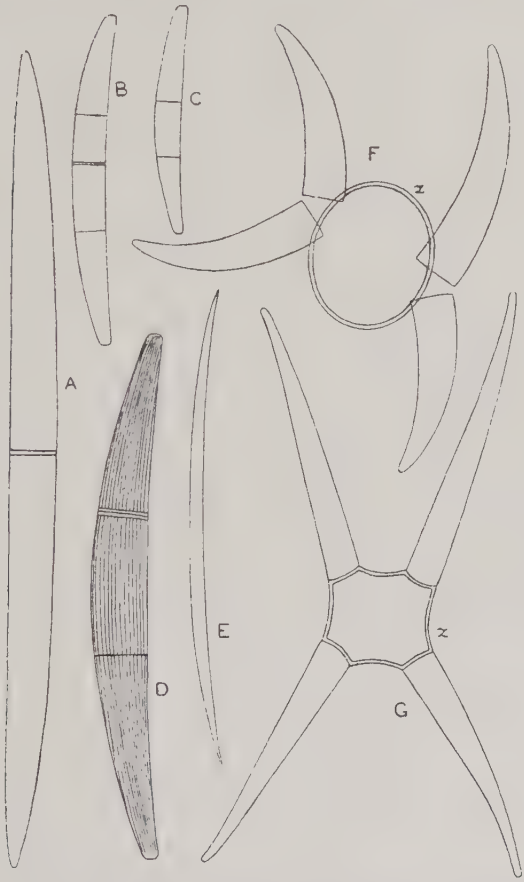

Fig. 106. A, *Closterium acerosum* (Schrank) Ehrenb., from Glen Shee, Perthshire (×200). B–D, *C. striolatum* Ehrenb., from Frensham, Surrey; B and C, outlines, ×125; D, ×260. E, *C. acutum* Bréb., from Sligachan, Skye (×474). F, *C. parvulum* Naeg., zygospore, from Esher West-end Common, Surrey (×474). G, *C. rostratum* Ehrenb. var. *brevirostratum* West, zygospore, from Wimbledon Common, Surrey (×200).

C. pusillum Hantzsch var. *monolithum* Wittr. (7·5–8·6 br.; 29·8–40·4 l.). *C. aciculare* Tuffen West and *C. pronum* Bréb. have very elongate cells, whilst certain forms of *C. acutum* Bréb. (fig. 106, E) are among the narrowest. In *C. Libellula* Focke (38–51 br.; 250–354 l.)

(fig. 105, D) the cells are not curved and both margins are convex. The commonest and most widely distributed sp. are *C. parvulum* Naeg. (fig. 106, F), *C. Venus* Kütz. with an angular and sometimes twisted zygosp., *C. Leibleinii* Kütz. (fig. 103, B), *C. moniliferum* (Bory) Ehrenb., *C. Ehrenbergii* Menegh. (fig. 103, A), and *C. acerosum* (Schrank) Ehrenb. (fig. 106, A). *C. gracile* Bréb. is often abundant in *Sphagnum*-bogs. The commonest striated sp. are *C. striolatum* Ehrenb. (fig. 106, B–D) and *C. rostratum* Ehrenb. Double zygosp. are found in *C. lineatum* Ehrenb. (fig. 104, F).

Sub-family 3. Cosmarieae

Docidium Brébisson, 1844; emend. Lundell, 1871. Cells comparatively small, slightly constricted, elongate, straight, subcylindrical, with an inflation on each side of the constriction or nodulose from pole to pole, apices always truncate and smooth; end-view circular. Chiefly distinguished from *Pleurotaenium* by the base of each semicell being plicated with a small granule at the base of each plication. Chloropl. axile, one in each semicell, with several irregular ridges and a median row of pyrens. Zygosp. unknown.

Of the three Brit. sp. *D. Baculum* Bréb. is alone widely distributed and even it is distinctly rare (12–13 br.; 167–262 l.) (fig. 107, A–C). *D. undulatum* Bail., which is restricted to the western districts of Ireland and Scotland, has semicells which appear nodulose owing to repeated shallow constrictions (13–16 br.; 187–262 l.) (fig. 107, D and E).

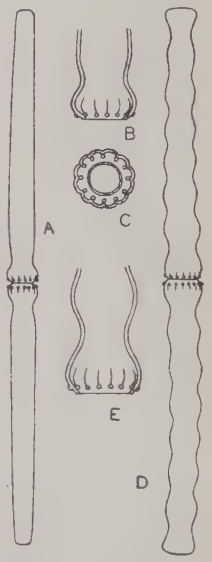

Fig. 107. A–C, *Docidium Baculum* Bréb., from Bowness, Westmorland; A, ×315; B, base of semicell, ×630; C, basal view of semicell, ×630. D and E, *D. undulatum* Bail., from near Oughterard, Galway, Ireland; D, ×315; E, base of semicell, ×630.

Pleurotaenium Naegeli, 1849[1]. Cells slightly constricted, elongate, straight, cylindrical, slightly attenuated towards each pole, with or without inflations on either side of the constriction, sometimes nodulose along their whole length, without basal plication of semicells; apices usually truncate, often furnished with a ring of conical granules or teeth; end-view circular. Chloropl. several in each semicell, disposed as longit. parietal bands furnished with a number of pyrens.,

[1] Naegeli, 1849, p. 104.

sometimes broken up into numerous parietal pieces each with one pyren. According to Carter[1] in *P. Trabecula* var. *rectum* there are two axile chloropl., each with a single row of pyrens. Central portion of cell often with large vacs. which sometimes contain

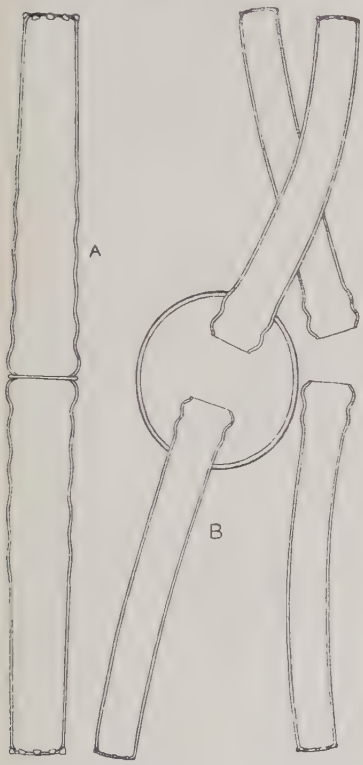

Fig. 108. A, *Pleurotaenium coronatum* (Bréb.) Rabenh., from Helvellyn, Cumberland (×236). B, zygospore of *P. Ehrenbergii* (Bréb.) De Bary, from Thursley Common, Surrey (×315).

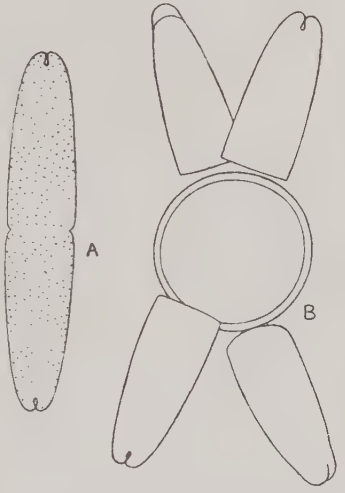

Fig. 109. *Tetmemorus granulatus* (Bréb.) Ralfs, from Lough Anna, Donegal, Ireland. A, front view of cell; B, zygospore (×315).

numerous moving granules (cf. p. 258). Zygosp. only known in a few sp., globose, smooth.

Sp. of this genus are much more abundant in the Tropics than in Temperate regions. Of the nine Brit. sp., *P. maximum* (Reinsch) Lund. is the largest, reaching a length of 852 μ and a breadth of 54 μ. The most abundant sp. is *P. Ehrenbergii* (Bréb.) De Bary (18–24 br.;

[1] loc. cit. 1919, p. 236.

240–400 l.) (fig. 108, B). *P. Trabecula* (Ehrenb.) Naeg. and *P. truncatum* (Bréb.) Naeg. are each widely distributed. *P. nodosum* (Bail.) Lund., a striking sp. in which the cells are provided with rings of nodules, is confined to the western districts of Wales, Ireland, and Scotland.

There is very little difference between this genus and *Docidium*, and Dr Carter's record of an axile chloropl. in a sp. of *Pleurotaenium* seems further to emphasise the close affinity between the two.

Tetmemorus Ralfs, 1844[1]. Cells slightly constricted, with deep apical clefts which are tightly closed, of moderate length, straight, usually attenuated towards each pole. Chloropl. one in each semicell, consisting of a central axis containing pyrens. and a number of longit. ridges, which in *T. Brebissonii* broaden out at the periphery into parietal bands. Zygosp. globose and smooth or subquadrate with rounded angles.

The four common sp. are well represented in the Brit. Isles. The most widely distributed are *T. granulatus* (Bréb.) Ralfs (30–45 br.; 138–238 l.) (fig. 109) and *T. laevis* (Kütz.) Ralfs (19–25 br.; 57–76 l.). The former is one of the most ubiquitous of Desmids, whilst the latter, which lacks the sparse scrobiculations on the wall, has a distinct preference for mountainous districts. *T. Brebissonii* (Menegh.) Ralfs, with subcylindrical cells, is frequent in bogs and pools containing submerged *Sphagnum*.

Euastrum Ehrenberg, 1832[2]. Cells relatively short, always distinctly flattened (end-view elliptical); in front-view general outline elliptical or narrowly elliptical, with a deep median constriction (sinus), entire or lobed lateral margins, and usually deeply notched apices. In the lobed sp. the number of lobes to each semicell is always uneven, the apical one which bears the notch being termed the *polar lobe*. There is generally a well-marked protuberance in the middle of each semicell just above the isthmus, most easily seen in the end- and side-views (fig. 110, A); in the more elaborate sp. there may be further symmetrically arranged protuberances. Chloropl. axile, one (two in *E. verrucosum*) in each semicell; in the smaller sp. consisting of a large central mass with a pyren. bearing four lobes which project outwards; in the larger of a thin axile portion and massive peripheral lobes spreading out as parietal plates beneath the wall and containing several scattered pyrens. Zygosp. globose or ellipsoid bearing numerous simple spines or conical papillae.

There are 44 Brit. sp., about half of which are widely distributed. The smallest and perhaps most abundant sp. is *E. binale* (Turp.) Ralfs (9–16 br.; 10–20 l.; 5·5–7 thick) (fig. 110). *E. elegans* Bréb. (fig. 110,

[1] Carter, loc. cit. 1919, p. 236.

[2] G. S. West, Journ. of Bot., 1912, p. 89; Carter, loc. cit. p. 237.

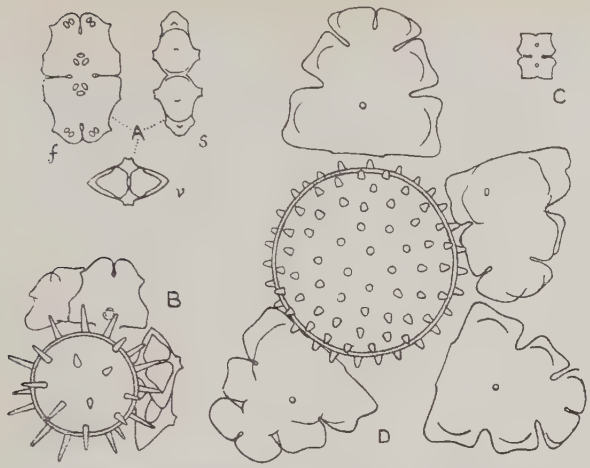

Fig. 110. A, *Euastrum elegans* (Bréb.) Kütz. (a form), from Capel Curig, N. Wales (×474). B, zygospore of *E. elegans*, from New Forest, Hants (×474). C, *E. binale* (Turp.) Ehrenb., from Thursley Common, Surrey (×474). D, zygospore of *E. oblongum* (Grev.) Ralfs, from Pilmoor, N. Yorks (×200). *f*, front-view; *s*, side-view; *v*, end-view.

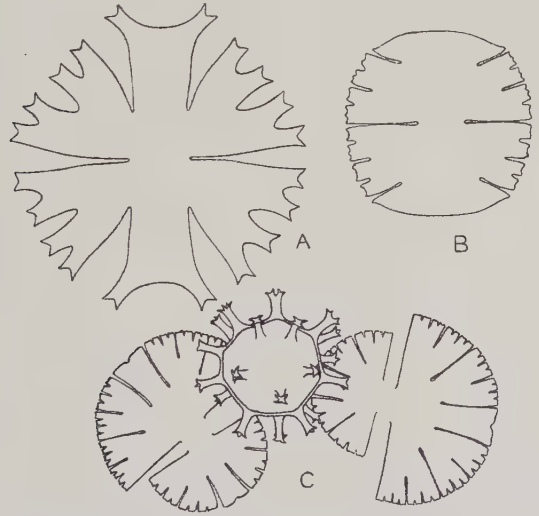

Fig. 111. A, *Micrasterias Crux-Melitensis* (Ehrenb.) Hass., from Bowness, Westmorland (×365). B, *M. truncata* (Corda) Bréb., from Thursley Common, Surrey (×200). C, zygospore of *M. denticulata* Bréb., from Halgavor Moor, Cornwall (×110).

A and B), *E. ansatum* Ralfs, *E. Didelta* (Turp.) Ralfs, and *E. oblongum* (Grev.) Ralfs (fig. 110, D) are widely distributed all over the country, but in some districts they are by no means common. *E. insigne* Hass. (46–60 br.; 98–110 l.) is an upland form found plentifully amongst *Sphagnum*. *E. verrucosum* Ehrenb. and *E. gemmatum* Ehrenb. are two of the most elaborately ornamented sp., whilst *E. crassum* (Bréb.) Kütz. (87–97 br.; 167–185 l.) and *E. oblongum* (80–83 br.; 144–167 l.) are the largest Brit. sp. *E. pectinatum* Bréb. is more frequently found with zygospores than any other sp. of the genus.

Micrasterias Agardh, 1827[1] (*Holocystis* Hassall, 1845; *Tetrachastrum* Dixon, 1859). Cells often large, flattened, in many cases almost disc-shaped, circular or broadly elliptical in outline, deeply constricted. Semicells divided by deep incisions into three or five lobes, the polar lobe being entire (fig. 111, B) or widely excavated (fig. 111, A); lateral lobes sometimes narrow and attenuated, but more frequently widening from the base outwards and divided by incisions of variable depth into lobules; flat surfaces sometimes furnished with spines or wart-like projections. Side- and end-views generally narrowly fusiform. Chloropl. one in each semicell, composed of a more or less distinct axile plate bearing a number of ridges which are developed to a varying extent according to the thickness of the cell; pyrens. many, scattered. Zygosp. globose, with strong spines, simple or furcate at the apex.

None of the 16 Brit. sp. is really abundant, although *M. denticulata* Bréb. (185–276 br.; 205–350 l.) (fig. 111, C) and *M. truncata* (Corda) Bréb. (90–129 br.; 100–138 l.) (fig. 111, B) are widely distributed. *M. rotata* (Grev.) Ralfs (195–220 br.; 220–240 l.) and *M. papillifera* Bréb. (115–145 br.; 135–145 l.) are not uncommon in permanent boggy pools and lakes, whilst *M. oscitans* Ralfs var. *mucronata* (Dixon) Wille (fig. 103, C, p. 256) and *M. Jenneri* Ralfs are frequently found in the *Sphagnum*-bogs of mountainous areas. *M. furcata* Ag., *M. Crux-Melitensis* (Ehrenb.) Hass. (fig. 111, A), and *M. pinnatifida* (Kütz.) Ralfs are amongst the rarest and most elegant sp.

Cosmarium Corda, 1834[2] (*Dysphinctium* Naegeli, 1849; *Calocylindrus* (Naegeli) Kirchner, 1878; *Cosmaridium* Gay, 1884; *Pleurotaeniopsis* (Lund.) Lagerheim, 1887). Cells relatively short (length rarely more than one and a half times the breadth), with a median constriction of varying depth; semicells circular, elliptical, semicircular, ovate, pyramidate, or cuneiform in front-

[1] Carter, loc. cit. 1919, p. 295.

[2] Klebahn, Jahrb. Wiss. Bot. XXII, 1891, p. 424; Comère, Bull. Soc. Bot. France, LIV, 1907, p. xlii; Nieuwland, Amer. Midland Naturalist, I, 1909, p. 4; Carter, loc. cit. 1920, p. 265.

view, apex rounded or broadly truncate without a notch. Cell-wall smooth, scrobiculate, granulate, verrucose, or clothed with minute spines, ornamentation often showing a definite arrangement. End-view circular or elliptical, but in many sp. there is a prominent protuberance in the middle of each semicell and in these the elliptical end-view is furnished on each side with a

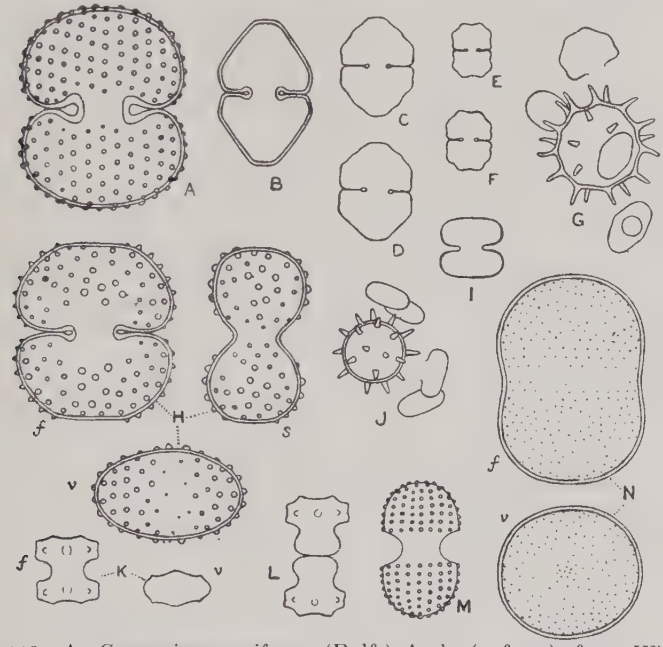

Fig. 112. A, *Cosmarium reniforme* (Ralfs) Arch. (a form), from Wicken Fen, Cambs. B, *C. granatum* Bréb., from Chippenham Fen, Cambs. C and D, *C. granatum* var. *subgranatum* Nordst., from Hornsey Mere, E. Yorks. E–G, *C. Meneghinii* Bréb.; E and F, from Hornsey Mere, E. Yorks; G, zygospore of a form, from Bowness, Westmorland. H, *C. praemorsum* Bréb., from Carrantuohill, Kerry, Ireland. I and J, *C. bioculatum* Bréb.; I, from Roswell Pits, Cambs; J, zygospore from Puttenham Common, Surrey. K and L, forms of *C. Regnesii* Reinsch; L shows one stage of cell-division. M, *C. isthmium* West, from Harris, Outer Hebrides. N, *C. pseudoconnatum* Nordst., from Capel Curig, N. Wales. (L ×1170, all other figs. ×473.) *f*, front-view; *s*, side-view; *v*, end-view.

distinct swelling (fig. 112, G). Chloropl. (fig. 102, F–I) usually axile, either one or two per semicell, each composed of a central axis giving rise to variously shaped radiating processes (ridges, plates, or string-like outgrowths) which sometimes enlarge into parietal masses at the periphery; usually with a single pyren. (sometimes divided) in the axis of each chloropl. In a few sp.

chloropl. entirely parietal (4–8 per semicell), each with one or more pyrens. Zygosp. globose, angular-globose, cubical, etc.; membrane smooth, scrobiculate, furnished with simple or furcate spines of variable length, or adorned with conical papillae; black in a few sp. (e.g. *C. melanosporum* Arch.).

This is the largest genus of Desmids, embracing at least seven or eight hundred well founded sp., and attempts to split it up into a number of smaller genera have frequently been made. Naegeli's *Dysphinctium* (=*Calocylindrus* Kirchn.), established for the sp. with rounded poles and but a slight constriction in front-view and an oval or circular end-view, is still maintained by some algologists, although it is practically impossible to delimit it from the main mass of sp. of *Cosmarium*. It is even less feasible to maintain the genus *Pleurotaeniopsis*, founded for the sp. with parietal chloropl., since Dr Carter's investigations altogether support the view of G. S. West that "the parietal condition has been independently acquired in *Cosmarium* by a few scattered members of the genus" (1904, p. 168). In view of the difficulty already existing of delimiting *Cosmarium* from *Euastrum* and *Xanthidium* on the one hand and *Staurastrum* on the other, it is inadvisable in the present state of our knowledge to attempt the establishment of further genera.

There are some 250 Brit. sp. of *Cosmarium*, and it is consequently scarcely possible to point out even the commoner characteristics in the small space available. The largest Brit. sp., and also one of the rarest, is *C. ovale* Ralfs (100–107 br.; 182–188 l.); the smallest is *C. subretusiforme* W. & G. S. West (6·2–6·5 br.; 7·8–8 l.). The number of sp. having a circular end-view is not very considerable; examples are *C. pseudoconnatum* Nordst. (fig. 112, N), *C. cucurbitinum* (Biss.) Lütkem. (*Penium cucurbitinum* Biss.) (fig. 103, D), and *C. curtum* (Bréb.) Ralfs (*Penium curtum* Bréb.) (fig. 105, F). *C. docidioides* Lütkem. (*Penium minutum* W. & G. S. West) is more elongate than any other Brit. sp. and also has a circular end-view. *C. Cucumis* Corda and *C. ovale* Ralfs are sp. with parietal chloropl. Fig. 112 gives a slight idea of the range of form and the diverse ornamentation of the wall, which is however not as complex in Brit. sp. as in many known from other parts of the world.

The commonest sp. found in the ponds and ditches of lowland districts are *C. Botrytis* (Bory) Menegh., *C. praemorsum* Bréb. (fig. 112, H), *C. subcostatum* Nordst., *C. humile* Gay, *C. granatum* Bréb. var. *subgranatum* Nordst. (fig. 112, C and D), *C. abbreviatum* Racib., and several forms of *C. Meneghinii* Bréb. (fig. 112, E–G). In the bogs of moorland districts *C. Cucurbita* Bréb. is usually abundant, and in upland *Sphagnum*-areas *C. Ralfsii* Bréb., *C. pyramidatum* Bréb., *C. subtumidum* Nordst., etc. are fairly general. Some sp., such as *C. Holmiense* Lund., *C. anceps* Lund., *C. subspeciosum* Nordst., and *C. Pokornyanum* (Grun.) W. & G. S. West are usually found on dripping rocks, whilst *C. Dovrense* Nordst., *C. microsphinctum* Nordst.,

etc. prefer wet calcareous rocks. *C. pygmaeum* Arch. sometimes occurs in myriads amongst the leaves of submerged *Sphagnum*.

Xanthidium Ehrenberg, 1834[1]. Cells somewhat flattened, with a deep median constriction. Semicells elliptical, trapeziform, hexagonal, or octagonal in front-view, the angles furnished with simple or furcate spines (chief distinction from *Cosmarium*) which are arranged in one or in two parallel planes and in a few sp. are of very minute dimensions; centre of each semicell with a thickened scrobiculate area or protuberance of variable size (sole distinction from *Arthrodesmus*). Chloropl. sometimes axile,

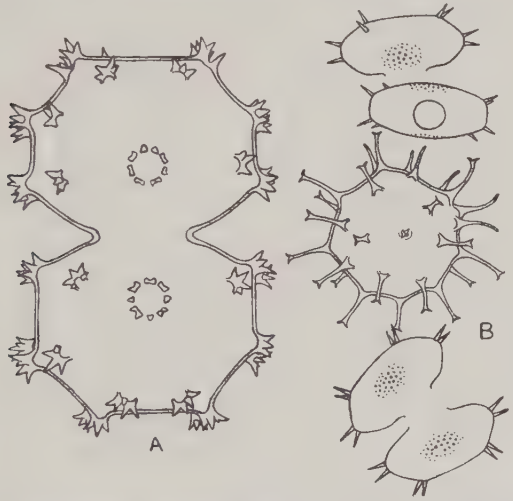

Fig. 113. A, *Xanthidium armatum* (Bréb.) Rabenh., from Sligachan, Skye (×365). B, zygospore of *X. antilopaeum* (Bréb.) Kütz., from Ballynahinch, Galway, Ireland (×365).

resembling those of *Cosmarium*, one or more commonly two per semicell (fig. 102, D), each with one pyren.; or more usually parietal and then generally four per semicell (fig. 102, E), again each with one pyren. (numerous scattered pyrens. in *X. armatum*). Zygosp. globose, adorned with blunt papillae or long slender spines which are simple or furcate at the ends.

Lundell[2] in 1871 divided the genus into the subgenera *Holacanthum* and *Schizacanthum* according as the spines were entire or branched at the apex, but the distinction is rather difficult to maintain, as in some of the tropical sp. there are numerous intermediate stages between simple and much-forked spines.

[1] Carter, loc. cit. 1919, p. 245.
[2] Lundell, Nov. Act. Reg. Soc. Sci. Upsala, ser. 3, VIII, 1871, p. 74.

There are 14 Brit. sp., of which a few are general but not abundant, and the rest are very scarce; they are regular constituents of the freshwater plankton. *X. armatum* (Bréb.) Rabenh. (88–110 br. with spines; 137–200 l. with spines) (fig. 113, A) is a large and handsome Desmid, occurring in moderate quantity in the bogs of hilly districts. *X. antilopaeum* (Bréb.) Kütz. (fig. 113, B) and *X. cristatum* Bréb. are not uncommon in certain areas. *X. concinnum* Arch., which is the smallest sp. (9·5–10·5 br. with apiculations; 9–9·5 l.), sometimes occurs abundantly amongst *Sphagnum*.

Arthrodesmus Ehrenberg, 1838. Primarily distinguished from *Xanthidium* by absence of protuberance or scrobiculated area in centre of semicells; spines usually fewer in number and all in one plane, one or two of variable strength arising from the lateral angles of the elliptical, trapeziform, or subhexagonal semicells; median constriction deep. End-view always elliptical,

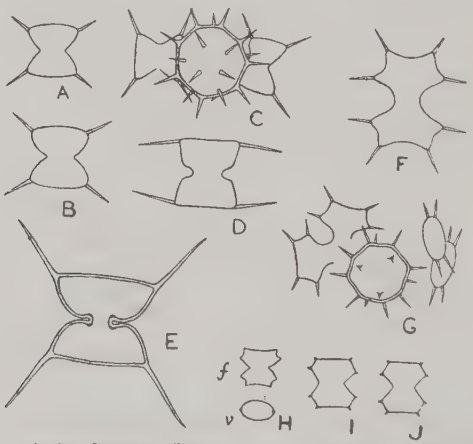

Fig. 114. A–C, *Arthrodesmus Incus* (Bréb.) Hass., from Harrop Tarn, Cumberland; C, zygospore (×365). D, *A. Incus* var. *Ralfsii* W. & G. S. West, from Capel Curig, N. Wales (×365). E, *A. Incus* var. *validus* W. & G. S. West (a form), from near Glenties, Donegal, Ireland (×474). F and G, *A. octocornis* Ehrenb.; F, from Llyn Idwal, N. Wales; G, zygospore, from Puttenham Common, Surrey (×474). H–J, *A. bifidus* Bréb. var. *truncatus* West; H, from Strensall Common, N. Yorks; I and J, from Keston Common, Kent (×474). *f*, front-view; *v*, end-view.

with spines at the poles. Chloropl. axile, one in each semicell, with one or two pyrens. Zygosp. globular, smooth, or clothed with simple, conical, or subulate spines.

Of the 11 Brit. sp., *A. Incus* (Bréb.) Hass. (fig. 114, A–C) is the only one that is general and abundant. It is very variable, frequently found conjugating, and of small dimensions (13–28 br. without spines; 13–33 l. without spines; spines 5–32 l.). *A. convergens* Ehrenb. and

A. octocornis Ehrenb. (fig. 114, F and G) are also not uncommon, but the other sp. are all rare.

Staurastrum Meyen, 1829[1]. Cells usually deeply constricted, with semicells which are elliptical, semicircular, oblong, or

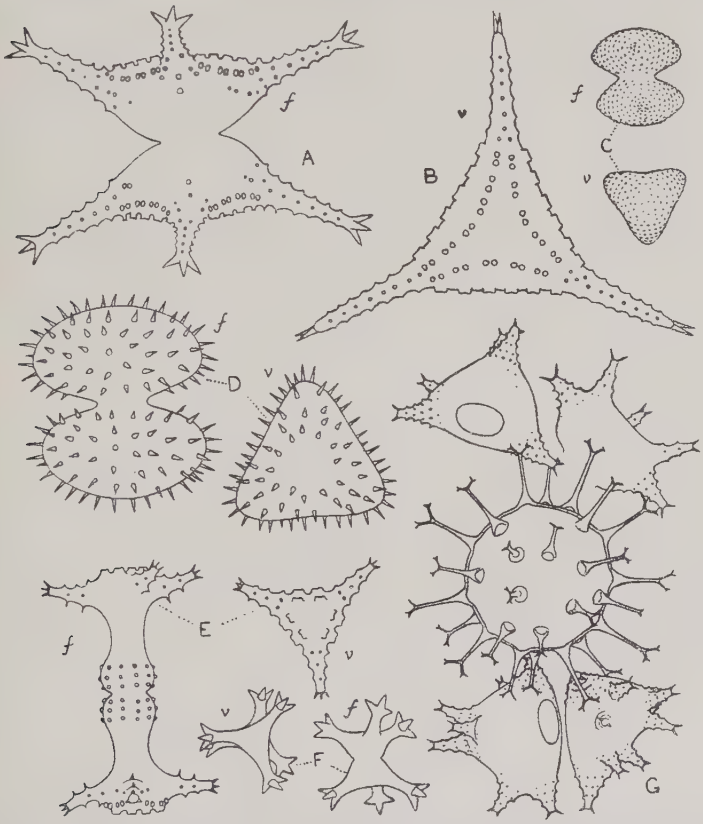

Fig. 115. A and B, *Staurastrum anatinum* Cooke and Wills, from Llyn-y-cwm-ffynon, N. Wales (×473). C, *S. punctulatum* Bréb., from Esher Common, Surrey (×473). D, *S. polytrichum* Perty, from Galway, Ireland (×365). E, *S. elongatum* Barker, from Rhiconich, Sutherland (×473). F, *S. brachiatum* Ralfs, from Down, Ireland (×473). G, zygospore of *S. furcigerum* Bréb., from Pilmoor, N. Yorks (×473). *f*, front-view; *v*, end-view.

cyathiform in front-view, and triangular, or more rarely 4-angular or polygonal in end-view; angles of the two semicells often alternating with one another, sometimes rounded, sometimes

[1] Millardet, Mém. Soc. sci. nat. Strasbourg, VI, 1870, p. 40; Carter, loc. cit. 1920, p. 303.

acute, in many sp. produced into processes of considerable length, generally furnished with two or three strong diverging spines at their ends. Cell-wall smooth or more frequently adorned with a variety of spines or wart-like excrescences which are usually symmetrically disposed. Chloropl. mostly axile, one per semicell, consisting of a central mass with a bilobed extension into each angle of the semicell (fig. 103, E) and a single central pyren. (or several more peripheral pyrens. in some of the larger sp.); in a few sp. there are a number of parietal chloropl. in each semicell, but intermediate states between this condition and the axile chloropl. are not uncommon. Zygosp. globose or angular, rarely winged, more commonly clothed with simple or furcate spines, each often situated at the apex of a mammillate or obtusely conical protuberance.

The sub-genus *Pleurenterium*[1], established for the sp. having parietal chloropl., leads to the grouping together of forms which are probably not closely allied. Parietal chloropl. are perhaps merely an outcome of increase in the size of the cells.

Staurastrum is the second largest genus of Desmids including some 600 sp., about 160 of which are known to occur in the Brit. Isles: few of them, however, are abundant. One of the largest sp. is *S. tumidum* Bréb. (91–103 br.; 112–132 l.; parietal chloropl.) and the smallest is *S. iotanum* Wolle. The most frequent sp. in low-lying districts are *S. pygmaeum* Bréb., *S. punctulatum* Bréb. (fig. 115, C), and *S. hexacerum* (Ehrenb.) Wittr. In moorland areas *S. margaritaceum* (Ehrenb.) Menegh. is general. The most abundant of the spiny sp. is *S. teliferum* Ralfs. Sp. like *S. capitulum* Bréb., *S. pileolatum* Bréb., *S. Kjellmani* Wille (fig. 103, E), *S. acarides* Nordst., and *S. Arnellii* Boldt are principally confined to mountainous regions; others, such as *S. pelagicum* W. & G. S. West, *S. pseudopelagicum* W. & G. S. West, *S. jaculiferum* West, *S. paradoxum* Meyen var. *longipes* Nordst., *S. brevispinum* Bréb., and forms of *S. anatinum* Cooke and Wills (fig. 115, A and B), are abundant in the plankton of lakes. A few of the most beautiful sp. (e.g. *S. Ophiura* Lund., *S. Cerastes* Lund., *S. Arctiscon* (Ehrenb.) Lund., *S. verticillatum* Arch., and *S. longispinum* (Bail.) Arch.) are confined to the Lake District and the extreme western districts of Scotland, Wales, and Ireland, being most abundant in the plankton of these areas.

Cosmocladium de Brébisson, 1856[2]. Colonial; cells resembling a smooth *Cosmarium*, but united by relatively thin single or double mucilage-threads attached near the sinus to form branched microscopic colonies which are sometimes enveloped in a mass of mucilage of lesser density than the connecting

[1] Lundell, loc. cit. p. 72.
[2] Schröder, Ber. Deutsch. Bot. Ges. XVIII, 1900, p. 15.

threads. Chloropl. axile, usually one in each semicell, with four projecting lobes and a single pyren., rarely only one chloropl. in the whole cell. Zygosp. globose and smooth, or irregular in shape (as in *C. perissum* Roy and Biss. (fig. 116, C)).

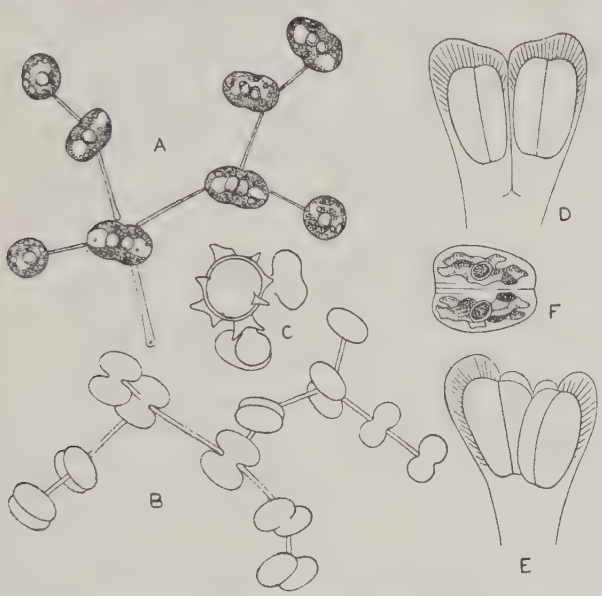

Fig. 116. A, *Cosmocladium constrictum* (Arch.) Josh., from Pilmoor, N. Yorks (×475). B, *C. pulchellum* Bréb., from near Tarbert, Harris, Outer Hebrides (×475). C, zygospore of *C. perissum* Roy and Biss., from the Clova Mts., Forfar (×475). D–F, *Oocardium stratum* Naeg., after Lütkemüller (×730).

All the five Brit. sp. are very rare. *C. constrictum* (Arch.) Josh. (fig. 116, A) and *C. pulchellum* Bréb. (fig. 116, B) are perhaps more often observed than the others. All the sp. are very small, the largest being *C. Saxonicum* De Bary (13·5–14·5 br.; 15–17 l.).

Oocardium Naegeli, 1849[1]. Colonial; cells small, in front-view slightly constricted, much broader than long, unequally depressed on the two sides, so that there are only two planes of symmetry; end-view broadly elliptical. Colonies generally hemispherical, 1–2 mm. in diam., composed of a number of dichotomously forked elongate tubes consisting of carbonate of lime occupied by mucilage, each widening towards the surface of the colony and enclosing at the free end a single cell with the longit. axis at right angles to the axis of the tube; the tubes are

[1] Naegeli, 1849, p. 74; Senn, Bot. Zeit. LVII, 1899, p. 81.

secreted by the cells occupying them. Chloropl. axile, one, situated on the broader side of each semicell, with a single pyren. Zygosp.[1] rectangular or polyhedral, with several mammillate projections.

The only known sp., *Oocardium stratum* Naeg. (fig. 116, D–F), is extremely rare and has only been recorded from the limestone districts of W. Yorks attached to rocks and stones in the beds of several mountain streams, and from Ireland (cells 18–24 br.; 13–20 l.).

Sphaerozosma Corda, 1835. Cells small, joined at their apices by gelatinous cushions, traversed by minute rounded tubercles or short capitate processes, to form long filamentous colonies, often twisted and sometimes provided with a mucous investment; median constriction deep and narrow or widely open; semicells in front-view elliptical, oblong, or subrectangular, with elliptical end-view. One axile chloropl. in each semicell, with a single pyren. Zygosp. globose, rectangular, or oblong, smooth or furnished with subulate spines.

None of the five Brit. sp. is abundant. *S. vertebratum* Ralfs (21–24 br.; 19 l.) (fig. 117, C) is the largest, whilst *S. excavatum* Ralfs (fig. 117, D–F) and *S. granulatum* Roy and Biss. are the most widely distributed.

Onychonema Wallich, 1860[2]. Cells small, joined to form long flexible filaments by means of two capitate, asymmetrically disposed, processes at each apex, which overlap on to opposite faces of the adjacent cell (cf. fig. 117, G); median constriction deep and narrow; semicells in front-view elliptical or reniform, sometimes with strong lateral spines at each side; end-view elliptical. One axile chloropl. in each semicell, with a single pyren. Zygosp. globose, furnished with simple spines.

The two Brit. sp. are distinctly rare, the one most generally found being *O. filiforme* (Ehrenb.) Roy and Biss. (*O. Nordstedtianum* Turn.; 14·5–16 br.; 14–15 l.) (fig. 117, G–H).

Spondylosium de Brébisson, 1844 (*Leuronema* Wallich, 1860). Cells small or of medium size, united by their flat or concave apices (without special processes) to form filamentous colonies, occasionally twisted and often enveloped in copious mucilage; median constriction usually deep and linear; semicells of very variable form in front-view; end-view elliptical, triangular or trilobed. Chloropl. as in *Sphaerozosma*. Zygosp. globose, smooth, or with simple spines.

[1] Carter, Monogr. Brit. Desm., Ray Society, v, 1923, p. 205.
[2] Wallich, Ann. and Mag. Nat. Hist., ser. 3, v, 1860, p. 194.

The three genera *Sphaerozosma*, *Onychonema*, and *Spondylosium* are solely distinguished by the mode of junction of the cells, and their retention is a matter of convenience.

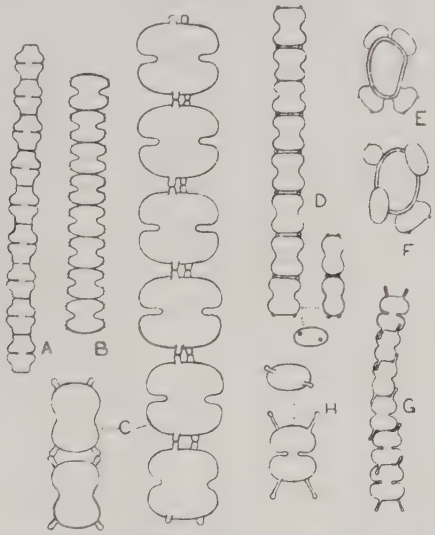

Fig. 117. A, *Spondylosium pulchellum* Arch., from Glen Shee, Perthshire (×365). B, *S. papillosum* W. & G. S. West, from Skipwith Common, E. Yorks (×475). C, *Sphaerozosma vertebratum* Ralfs, from near Crowan, Cornwall (×475). D–F, *S. excavatum* Ralfs; D, from Llyn Idwal, N. Wales (×475); E, zygospore, from Puttenham Common, Surrey (×475); F, zygospore, from New Forest, Hants (×475). G–H, *Onychonema filiforme* (Ehrenb.) Roy and Biss., from Strensall Common, N. Yorks (G, ×475; H, ×730).

None of the eight sp. of *Spondylosium* known to occur in the Brit. Islands is abundant. *S. papillosum* W. & G. S. West (9·5–10·5 br.; 8–9·5 l.) (fig. 117, B) and *S. pulchellum* Arch. (11–12·5 br.; 12·5–15 l.) (fig. 117, A) are the most widely distributed.

Hyalotheca Ehrenberg, 1841[1]. Cells more or less cylindrical, connected by their broadly truncate apices into filamentous colonies, usually twisted and mostly with a thick mucilage-envelope; median constriction very slight; semicells in front-view trapezoid, subquadrate or oblong, with straight or convex lateral margins; end-view circular, often with two or three nipple-like projections at equal intervals round the margin due to slight swellings at the base of the semicell. Chloropl. one in each semicell, consisting of a central mass with one or more pyrens. and a number of radiating plates. Zygosp. globose, smooth; parthenospores also known.

[1] Acton, Ann. of Bot. xxx, 1916, p. 380.

There are five Brit. sp., of which *H. dissiliens* (Sm.) Bréb. (fig. 118, A–D) is general and often abundant; cells 21–33 br., 15–25 l.; its zygosp., which are surrounded by a cruciform structure formed from the four empty semicells, are more frequently found than those of any other Desmid. *H. mucosa* (Mert.) Ehrenb. is much scarcer,

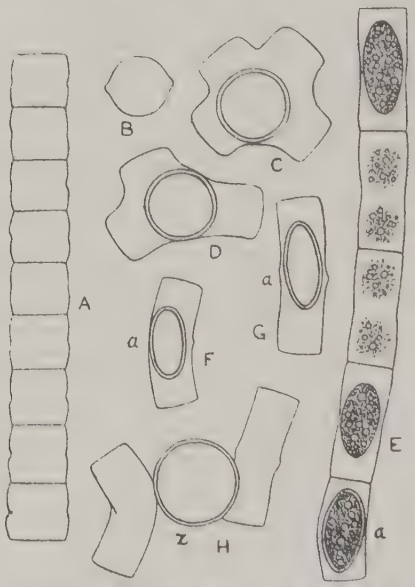

Fig. 118. A–D, *Hyalotheca dissiliens* (Sm.) Bréb.: A and B, from Capel Curig, N. Wales (×365); C and D, zygospores, from Galway, Ireland (×365). E–H, *H. neglecta* Racib., from the New Forest, Hants (×475); E–G, showing parthenospores (*a*); H, zygospore (*z*).

although widely distributed; it is distinguished by the absence of constriction and the presence of a crown of minute apical granules. *H. undulata* Nordst. (7·5–9 br.; 13·5–17·5 l.) and *H. neglecta* Racib. (11·5–13 br.; 28–34·5 l.) (fig. 118, E–H) are amongst the rarest of Brit. Desmids.

Desmidium Agardh, 1824 (*Didymoprium* Kützing, 1843; *Aptogonum* Ralfs, 1848). Cells generally much broader than long, united by their flat apices or by corresponding truncate apical projections (leaving a space of variable width between the actual apices) to form twisted filamentous colonies, often enveloped in a wide mucous coat; median constriction moderately deep; semicells usually much depressed, the end-view being triangular, quadrangular, or elliptical with mammillate poles. The septa, soon after their formation, develop on either side a cylindrical ring-

like ingrowth similar to that found in sp. of *Spirogyra* with replicate end-walls (fig. 119, B); as the young semicells enlarge, these invaginations become protruded to form their contiguous apices[1]. Chloropl. axile, one in each semicell, with as many pyrens, as there are angles in the end-view and with two plates extending into each angle (cf. *Staurastrum*). Zygosp. rounded

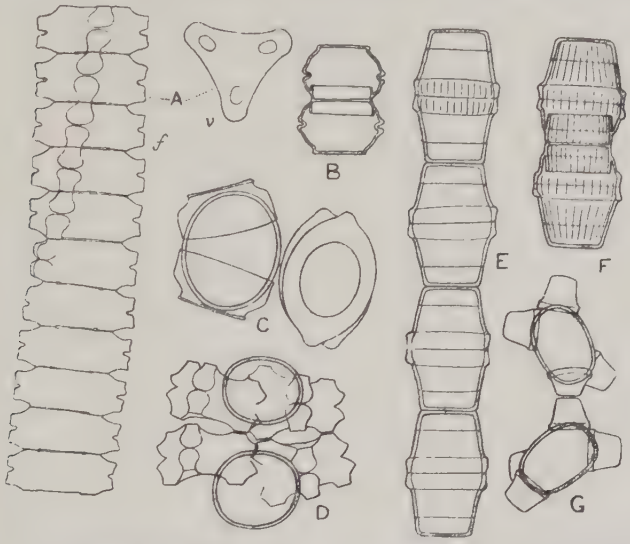

Fig. 119. A, *Desmidium Swartzii* Ag., from near Preston, Lancs (×365). B, *D. quadratum* Nordst., showing septum between two individuals (×475). C, zygospore of *D. cylindricum* Grev., from Donegal, Ireland (×350). D, zygospores of *D. Aptogonum* Bréb. (×475). E and F, *Gymnozyga moniliformis* Ehrenb., from Rhiconich, Sutherland (×475); F, two cells with intervening septum. G, zygospores of *G. moniliformis* var. *gracilescens* Nordst. (×475). *f*, front-view; *v*, end-view.

or ellipsoidal, smooth or furnished with somewhat flattened or conical papillae.

There are eight Brit. sp., none of which is abundant. *D. Swartzii* Ag. (37–43 br.; 14–19 l.) (fig. 119, A) and *D. cylindricum* Grev. (*Didymoprium Grevillii* Kütz.) (fig. 119, C) are the most general, the latter being the only Desmid in which the zygosp. is formed in one of the conjug. cells. *D. quadratum* Nordst. (fig. 119, B) and *D. graciliceps* (Nordst.) Lagerh. are very rarely met with.

Gymnozyga Ehrenberg, 1840 (*Bambusina* Kützing, 1845). Cells cylindrical or barrel-shaped, united by the flat ends into slightly twisted filamentous colonies; median constriction

[1] cf. De Bary, 1858, p. 44.

slight; semicells provided with a basal swelling of variable size; end-view circular, sometimes with two opposite papillae; cell-wall frequently with delicate longit. grooves; division and septa (fig. 119, F) as in *Desmidium*[1]. Chloropl. axile, one in each semicell, with a single pyren. and six radiating plates. Zygosp. oval or subglobose, smooth.

The only Brit. sp. is *G. moniliformis* Ehrenb. (*Desmidium Borreri* Ralfs; *Bambusina Brebissonii* Kütz.; 17·5–22·5 br.; 25–30 l.) (fig. 119, E) which is generally distributed in boggy districts, particularly in elevated localities.

GROUP 7. SIPHONALES

The outstanding feature of the Siphonales is the rare production of septa, the variously branched filaments of which the thallus is usually composed affording the most typical examples of coenocytic construction to be found among the Algae. The structure of these filaments is, generally speaking, of a uniform plan throughout the group. The cytoplasm forms a moderately thick lining layer beneath the wall and bounds a continuous central cavity occupied by sap; where special mechanical devices are absent, as for instance in the common *Vaucheria*, the filaments consequently collapse as soon as the protoplasm is killed and turgor no longer comes into play. Within the lining cytoplasm are situated many discoid chloroplasts, commonly possessing pyrenoids (but not in Vaucheriaceae), whilst internal to them are found numerous small nuclei.

The vast majority of the Siphonales inhabit the sea, more especially in the warmer regions of the earth, and the only freshwater representatives are the Vaucheriaceae[2], which possess at the same time the simplest vegetative construction and the most advanced reproductive mechanisms. The vigorous development of the group in a marine environment is exemplified by *Bryopsis* and *Caulerpa* with their high morphological differentiation, the Codiaceae with a compact thallus composed of closely apposed and intertwined coenocytic threads, and the elaborately organised Dasycladaceae with a plant-body built up by dense aggregation of whorled branches. Many members of the last two families are abundantly encrusted with carbonate of lime[3] and play a part in the formation of marine calcareous deposits, a rôle which they have evidently fulfilled since remote ages, as

[1] cf. De Bary, 1858, p. 44.

[2] There are also the Phyllosiphonaceae, parasitic on the leaves of tropical Phanerogams (cf. p. 58).

[3] cf. also Kolkwitz and Kolbe, Ber. Deutsch. Bot. Ges. XLI, 1923, p. 312.

a considerable number of fossil forms are known from the Carboniferous period.

A coenocytic tendency is well-marked among some zoosporic Chlorococcales (cf. p. 98)[1] and this probably led to the evolution of types like *Protosiphon* (p. 111). It is quite plausible to regard such a form as illustrative of the starting-point of the Siphonales[2]. An origin other than that from Chlorococcales would seem improbable, although Oltmanns (1922, p. 429) believes in a reduction from forms like Cladophorales.

It is plain that a long history must intervene between the primitive members of Siphonales and the Vaucheriaceae with their oogamous reproduction. There is nothing equivalent among other Siphonales (although more or less marked anisogamy is not infrequent, *Bryopsis*, *Codium*), and the nearest parallel is in the writer's opinion[3] to be found among the oogamous Phycomycetes. The Vaucheriaceae are possibly an offshoot from the line of evolution of the latter. The reference of Vaucheriaceae to the Heterokontae, which was at one time advocated[4], can scarcely be supported, alone because of the obvious Isokontan characters of the genus *Dichotomosiphon*.

The only freshwater forms are included in the

Family VAUCHERIACEAE

This comprises the long familiar *Vaucheria* to which in 1902 Ernst's *Dichotomosiphon*[5], not yet recorded in the British Isles, was added. There is a single freshwater species of the latter, whilst the numerous species of *Vaucheria* are found, more particularly in temperate regions, on damp earth, in fresh and brackish water, and a few in the sea. The plants invariably appear as a felt of simple branching filaments with apical growth; in *Dichotomosiphon* they show dichotomy, as well as frequent local thickenings of the membrane at points where the filaments are slightly constricted, so that they closely resemble the threads composing the thallus of an *Udotea* (Codiaceae). The chloroplasts are invariably without pyrenoids and starch has only been encountered in *Dichotomosiphon*, the species of *Vaucheria*

[1] In *Phyllobium*, in which however evolution has taken place in the direction of space-parasitism, the plant-body in certain stages even adopts the habit of a branched coenocytic thread.

[2] Blackman and Tansley, 1903, p. 21.

[3] Fritsch, Science Progress, v, 1910, p. 94.

[4] Bohlin, Utkast gröna Alg. och Arkeg. Fylogeni, Upsala, 1901, p. 25; Blackman and Tansley, 1903, p. 58.

[5] Ernst, Beih. Bot. Centralbl. XIII, 1902, p. 115.

forming a kind of oil as a food-reserve[1]. Upon injury to the thallus septa usually arise cutting off the injured parts (fig. 120, A and B); otherwise septa are rarely formed except in connection with reproduction.

Prolific asexual reproduction of *Vaucheria* takes place by means of large multiciliate zoospores[2]. These are produced singly in club-shaped sporangia, cut off from the somewhat swollen ends of branches into which have passed numerous chloroplasts and nuclei (fig. 120, C). The septum arises in a transverse bridge of colourless cytoplasm which appears at the base of the young sporangium. Within the latter an inversion of the relative positions of chloroplasts and nuclei ensues, so that the latter take up a peripheral position, and this is followed by contraction of the contents and the protrusion of a pair of short equal cilia opposite each nucleus (fig. 3, A). By gelatinisation of the wall at the apex a narrow aperture is formed through which the large oval or pear-shaped zoospore pushes its way. Sometimes the part first protruded becomes separated from that still left in the sporangium and two zoospores are formed instead of one.

Each zoospore includes a central vacuole which is filled with sap and may be traversed by strands of cytoplasm, although the sporangia of other Siphonales produce numerous separate biciliate zoospores in the formation of which the central vacuole and its bounding membrane as usual play no part. There can be no doubt that the peculiar zoospore of *Vaucheria* is a compound structure representing a number of biciliate zoospores which have failed to separate. In *V. ornithocephala* Ag. cilia are stated to be fully developed only on that half of the synzoospore which is directed forwards[3]. Aplanospores, produced when the plants are exposed to drought, have been recorded in a number of species (e.g. *V. geminata* DC., *V. uncinata* Kütz.); in the marine *V. piloboloides* Thur. they may germinate within the sporangia, or the whole sporangium without contraction of contents may grow out into a new plant[4]. It is plain that all stages in the gradual elimination of the zoospore and its replacement by a motionless reproductive element are realised. In *Dichotomosiphon* no zoospores are formed, their place being taken by somewhat irregular club-shaped akinetes (gemmae) formed at the ends of special rhizoid-like branches, from which they become detached after the formation of a septum.

[1] According to Meyer (Ber. Deutsch. Bot. Ges. xxxvi, 1918, p. 239) this is not a true fat.

[2] cf. Strasburger, Zellbildung u. Zellteilung, 3 Aufl., 1880, p. 84; Berthold, Stud. üb. Protoplasmamechanik, 1886, p. 291; Klebs, 1896, p. 4.

[3] Goetz, Flora, lxxxiii, 1897, p. 94.

[4] Ernst, Beihefte Bot. Centralbl. xvi, 1904, p. 370.

The zoospores of *Vaucheria* generally escape in the morning or after the plants have been in darkness. According to Klebs (loc. cit.) they can always be obtained, if filaments kept moist for some days are soaked in water or removed from a dilute nutritive solution into pure water or transferred from running to still water. The zoospores are sluggish in their movements which continue only for about 15 minutes. On coming to rest the cilia are withdrawn and a thin cell-wall is developed; germination follows almost immediately by the protrusion of one or more tubular outgrowths (fig. 120, D), one of which often attaches itself to a substratum by a colourless branched rhizoid.

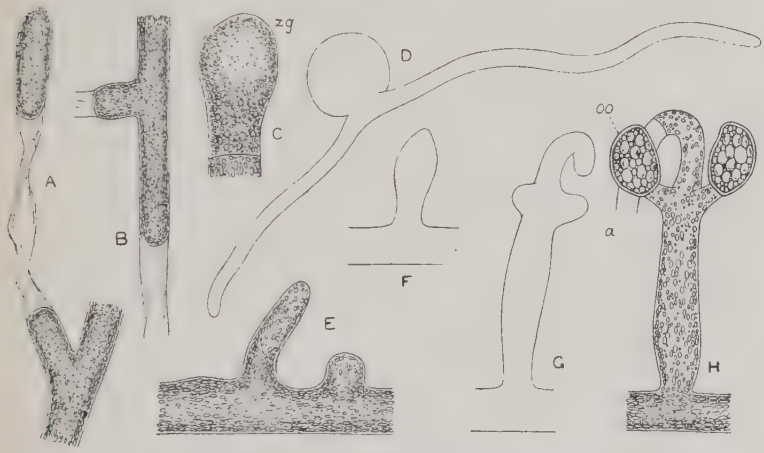

Fig. 120. A and B, portions of threads of *Vaucheria* showing formation of septa on injury. C, apex of filament of *V. sessilis* (Vauch.) DC. showing a sporangium (*zg*). D, germination of zoospore of *V. ornithocephala*, from E. Yorks. E, *V. sessilis*, from W. Yorks, showing developing oogonium (on right) and antheridium (on left). F–H, *V. geminata* (Vauch.) DC., from Barnes Common, Surrey, showing development of sexual organs. (All ×75.) *a*, antheridium; *oo*, oogonium.

Sometimes, owing to drought, the contents of the filaments break up into a number of pieces, each of which develops a thick stratified membrane and becomes replete with oil. The cysts thus formed may remain connected for a time by the membrane of the parent-filament, constituting the so-called *Gongrosira*-stages, which, however, have nothing to do with the genus *Gongrosira* described on p. 197.

The ordinary method of preparation for a resting period is by the production of oospores as a result of a sexual process which is of frequent occurrence in nature. The majority of the species are monoecious, antheridia and oogonia usually arising close

together at intervals along the threads; there is however considerable diversity of arrangement, even in different individuals of the same species. The development of the sexual organs has only been studied in a few forms[1].

The oogonia usually appear as sessile (fig. 121, A, B) or very shortly stalked lateral outgrowths of the main threads or, together with the antheridia, occur on special short branches (fig. 120, H). They soon assume a more or less rounded or ovate form and ultimately become cut off by a septum near the base. At this stage the oogonium is densely filled with oil and chloroplasts, but contains only a single central nucleus which gradually acquires quite considerable dimensions. The uninucleate condition is attained either by all but one of the nuclei returning to the main filament (Oltmanns, Heidinger) or by degeneration of all but one (Davis); possibly both methods obtain in different species. The maturation of the oogonium is usually marked by the development of a one-sided beak, the tip of which gelatinises and forms an aperture through which a small quantity of colourless cytoplasm is extruded (fig. 121, A); the single ovum possesses a colourless receptive spot opposite the opening.

The antheridia, which mostly develop simultaneously with the adjacent oogonia (fig. 120, E), are in general strongly curved cylindrical tubes which become cut off from the thread from which they arise by one or two septa (fig. 121, A, B). The nuclei of the antheridium undergo further subdivision and ultimately a small mass of cytoplasm becomes appropriated to each to constitute a spermatozoid; in the mature antheridium of *V. sessilis* the spindle-shaped spermatozoids form a radially arranged group between the central vacuole and unused peripheral cytoplasm containing the chloroplasts. Opening of the antheridia usually takes place apically (by several apertures in *V. Debaryana*) and with the sperms is expelled some of the waste cytoplasm. The male cells are exceedingly minute, quite colourless, and provided with two cilia, one pointing forwards and the other backwards (fig. 121, A). In many cases probably the adjacent oogonium is fertilised. After penetration of the spermatozoid a membrane first forms across the oogonial aperture; subsequent thickening-layers invest the whole oospore, within which further accumulation of oil takes place. Germination is direct, the contents giving rise to a new thread.

Wettstein[2] caused artificial parthenogenesis in *V. hamata* by pricking the mature oogonia.

[1] Oltmanns, Flora, LXXX, 1895, p. 388; Davis, Bot. Gaz. XXXVIII, 1904, p. 81; Heidinger, Ber. Deutsch. Bot. Ges. XXVI, 1908, p. 313.

[2] Wettstein, Ber. Deutsch. Bot. Ges. XXXVIII, 1920, p. 260.

In *Dichotomosiphon* the sexual organs occupy the ends of the final forking branchlets, each oogonium or antheridium being situated on a separate branch.

The compound zoospore of *Vaucheria* recalls the multinucleate gonidium of various Peronosporaceae, whilst the motionless aplanospores of the former and the gemmae of *Dichotomosiphon* constitute an even closer parallel. There are also many resemblances in the detailed structure of the sexual organs. These analogies lend support to the view, already mentioned above and first propounded by Lotsy, that the Vaucheriaceae represent an algal group parallel with the Phycomycetes and possibly having a common ancestry with them.

Vaucheria De Candolle, 1803[1]. Filaments interwoven to form compact mat-like masses on damp earth or in fresh or salt water, often very sparsely branched, some sp. rarely exhibiting any

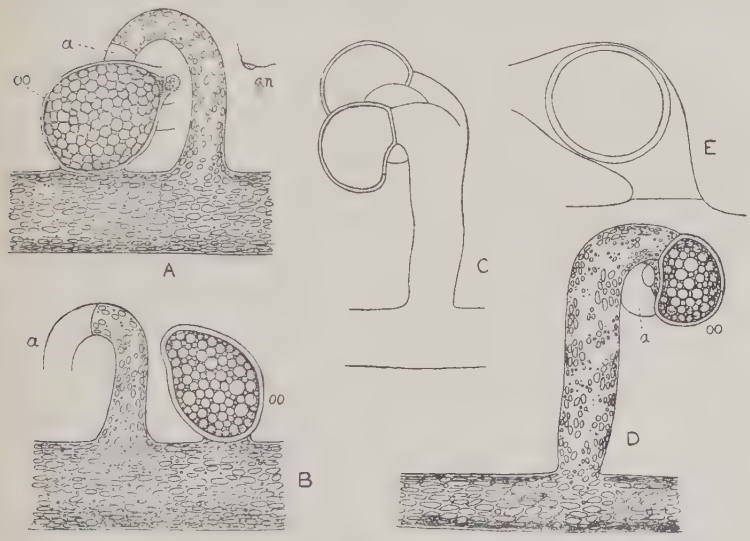

Fig. 121. A and B, *Vaucheria sessilis* (Vauch.) DC.; A, from Esher West-end Common, Surrey; B, from Mitcham Common, Surrey. C and D, *V. hamata* (Vauch.) Lyngb., from Calverley, W. Yorks. E, oogonium and oospore of *V. ornithocephala* Ag., from Beverley, E. Yorks. (A–D, ×200; E, ×320.) *a*, antheridium; *an*, spermatozoid; *oo*, oogonium.

branching except in connection with the formation of sexual organs. Filaments unseptate, coarse and thick, sometimes reaching 30 cm. in length, with a thin relatively weak membrane,

[1] Walz, Jahrb. Wiss. Bot. v, 1867, p. 127; Goetz, loc. cit. p. 88; Heering, Jahrb. Hamburg. Wiss. Anstalt. xxiv, 1906, p. 111; Heering, 1921, p. 76.

and dark green in colour owing to the numerous very small, oval, elliptical or subcircular chloropl. without pyrens.; small oil-drops abundant in the cytoplasm. Oogonia and antheridia usually adjoining, either sessile or on very short stalks on the main filaments, or several together on special short branches.

It is no easy matter to distinguish the sp. The main subdivisions are based largely on the characters of the antheridia, viz. (after Heering, 1921, p. 78):

I. *Woroninia*. Antherid. sessile, ovoid or club-shaped, dehiscing by a definite apical aperture (*V. dichotoma*).

II. *Tubuligerae*. Antherid. sessile, cylindrical, not curved, dehiscing by a slit (*V. aversa*).

III. *Globiferae*. Antherid. stalked, subspherical, stalk and antherid. forming a curved structure (*V. pachyderma*).

IV. *Corniculatae*. Antherid. stalked, shaped like a horn.

(*a*) *Sessiles*. Oogon. sessile on the thallus (*V. sessilis* (fig. 121, A, B)).

(*b*) *Racemosae*. Oogon. on special side branches terminated by an antherid. (*V. terrestris*, *V. geminata* (fig. 120, H), *V. hamata* (fig. 121, C, D)).

V. *Anomalae*. Antherid. with several apertures (*V. Debaryana*).

The majority of the common sp. belong to the Corniculatae. The sp. usually occur in situations where there is good aeration, i.e. where they are subject to the splashing or trickling of water, or in streams, although some habitually occur on damp ground; they are most abundant in the earlier months of the year. The threads are sometimes subject to the attacks of the Rotifer *Notommata Werneckii* which produces irregular gall-like swellings.

V. sessilis (Vauch.) DC. is perhaps the commonest sp., being widely distributed in damp and wet situations in the neighbourhood of streams, cataracts, and boggy springs; threads 65–80 br. (fig. 121, A and B). *V. geminata* (Vauch.) DC. occurs in similar localities; threads 78–90 br. (fig. 120, H). *V. terrestris* Lyngb. and *V. hamata* (Vauch.) Lyngb. (fig. 121, C and D) occur in profusion on damp ground, often forming thick mats on gravel paths and on the surface of soil of damp flower-pots. *V. ornithocephala* Ag. (*V. sericea* Lyngb.) (fig. 121, E), which is the smallest Brit. sp. (threads 48–55 br.), and *V. aversa* Hass. usually occur entirely submerged in the waters of ditches and ponds. *V. dichotoma* (Lyngb.) Ag. is the largest Brit. sp. (threads 180–220 br.) and is dioecious. Some forms of it are truly marine, but others occur in brackish water.

CLASS II. HETEROKONTAE

This class was first clearly distinguished by Luther[1] in 1899, although the close relationship between certain of the Algae included in it had been recognised much earlier by Borzi[2]. It was however the discovery of definite flagellate representatives (Heterochloridales) that paved the way to a proper comprehension of its distinctive features. As a matter of fact there is no other class in which a flagellate ancestry is as clearly patent as in this case, and it has contributed more than any other to the firm establishment of the doctrine of flagellate evolution of the Algae. The range of form encountered among Heterokontae shows an astonishing parallelism with that of Isokontae, but the total number of genera and species is far less.

The motile types of this class are purely flagellate and but few are known. They are well exemplified by *Chloramoeba*[3] (fig. 1, B), a naked unicell, hitherto encountered only in more or less brackish water and not yet found in this country. The living individuals have a very variable outline owing to the soft character of the periplast (p. 25). The front end is broad and more or less truncated and bears the two unequal cilia, which are characteristic of most Heterokontae. One cilium is about twice the length of the cell, whilst the other is a very short curved structure; beneath their point of attachment lies a contractile vacuole. The cells contain a single nucleus and 2–6 discoid chloroplasts, which are always devoid of pyrenoids and of a yellow-green colour owing to the presence of an excess of xanthophyll[4]. Such plastids are met with in all Heterokontae and are invariably associated with an absence of starch, drops of oil occurring as the usual reserve-food. These facts are probably indicative of a metabolism essentially different from that of Isokontae. Reproduction of *Chloramoeba* has not been observed, but is no doubt effected by longitudinal division as in other Flagellates. Ellipsoidal cysts with a thick membrane and filled with copious oil are readily produced. If supplied with organic nutriment, *Chloramoeba* can thrive for prolonged periods

[1] Luther, Bih. K. Sv. Vet.-Akad. Handl. xxiv, 1899, Afd. 3, No. 13, p. 17.

[2] Borzi, Stud. Algologici, Palermo, ii, 1895, p. 199; cf. also Braun, 1855, p. 49.

[3] Bohlin, 1897 *a*, p. 513.

[4] This is shown by the blue coloration resulting on heating with strong hydrochloric acid, a useful reaction for recognising doubtful members of Heterokontae.

in darkness and at such times becomes colourless (cf. *Polytoma*, p. 73; *Euglena*, p. 409). In Pascher's *Heterochloris*, another motile unicellular Heterokontan, there are two laterally placed chloroplasts in each cell.

No motile colonial types have so far become known in this class, but the palmelloid phase is well represented (Pascher's Heterocapsales), though the assignation of some of the genera included here is not altogether beyond doubt. *Chlorosaccus*[1] is however an undoubted palmelloid Heterokontan, occurring as pale yellow-green diffluent masses or hollow spheres attached to freshwater aquatics; it is a rare form not yet found in this country. The numerous pyriform cells, with two or more yellow-green chloroplasts (fig. 122, E), are arranged peripherally within the mucilage which is mainly composed of pectic substances. The cells multiply by longitudinal division and propagation is effected by typical Heterokontan swarmers with one long and one short cilium (fig. 122, F). Thick-walled cysts are also known. The relation of *Chlorosaccus* to *Chloramoeba* is very similar to that of a *Tetraspora* to *Chlamydomonas*, except that the motile individual in the former case is on a somewhat lower plane of development.

The Heterocapsales also include the common planktonic Alga *Botryococcus* (fig. 125), as well as *Askenasyella* (fig. 127, B, C), in both of which the cells contain only a single chloroplast, a rather exceptional condition among Heterokontae and not the only respect in which these genera stand rather apart. The dendroid type of colony is well illustrated by *Mischococcus* (fig. 124), a freshwater epiphyte, the uniciliate[2] zoospores of which secrete a tubular mucilage-stalk at their lower end, after coming to rest: as cell-division occurs, the products become separated by similar mucous stalks and, when a cell divides longitudinally, a kind of dichotomous branching is initiated.

A whole series of forms are known (Pascher's Heterococcales) which constitute the Heterokontan parallel to the Chlorococcales. These Heterococcales possess, in common with the Algae previously considered, the characteristic chloroplasts, oil as the product of assimilation, and, when present, typical swarmers with two unequal cilia. There is need to emphasise these facts, since the degree of similarity of outward form is in part astounding. Apart from the ordinary spherical type, such as *Chloro-*

[1] Luther, loc. cit. p. 3.

[2] In quite a number of the Heterokontan swarmers but a single cilium has been observed. It is generally assumed that the short one, which is often directed backwards and adpressed to the body, has been overlooked, but it is not at all unlikely that this cilium may have been completely eliminated in some cases.

botrys (fig. 128), we have *Botrydiopsis* (fig. 122, B) much resembling a small yellow-green *Eremosphaera*, *Characiopsis* (fig. 129) so similar to *Characium* that its species were long included in the latter, and Pascher's *Pseudotetraëdron*[1], closely parallel to *Tetraëdron*. The analogy goes further, since one can

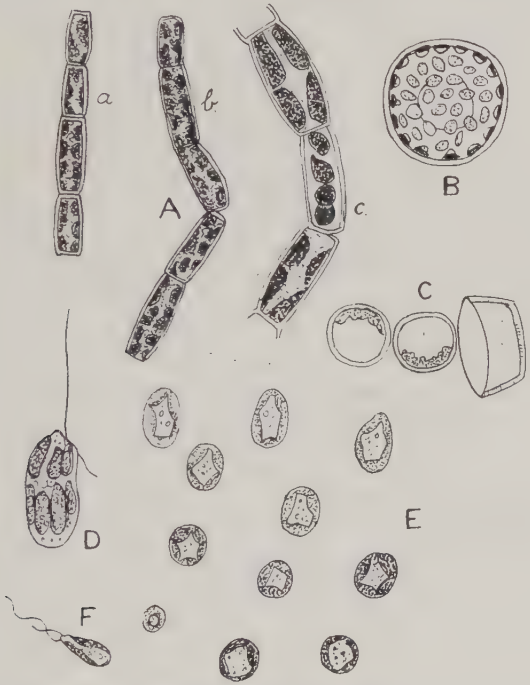

Fig. 122. A, *Bumilleria exilis* Klebs (after Bristol); *a* and *b*, vegetative threads (×720); *c*, the middle cell showing formation of zoospores (×1250). B, *Botrydiopsis arrhiza* Borzi (after Borzi, ×400). C, *Chlorobotrys regularis* (West) Bohlin, germinating cyst (after Bohlin, ×875). D, *Tribonema bombycinum* (Ag.) Derb. et Sol., zoospore (after Luther, ×640). E–F, *Chlorosaccus fluidus* Luther (after Luther, ×720); E, small part of a colony; F, zoospore.

distinguish a set of forms (*Chlorobotrys*, *Centritractus*), which appear to be azoosporic, from a set in which swarmers are the rule (*Characiopsis*, *Botrydiopsis*)[2]. It does not appear that this group has adapted itself as strikingly to a planktonic existence, as have the Chlorococcales among Isokontae. Pascher[3] has

[1] Pascher, Hedwigia, LIII, 1913, p. 1.

[2] cf. also Pascher, 1918, p. 399.

[3] Pascher, Ber. Deutsch. Bot. Ges. XXXIII, 1915, p. 488, and XXXV, 1917, p. 170.

however recently shown that two common oceanic plankton types, *Halosphaera*[1] and *Meringosphaera*, are members of the Heterococcales. Perhaps one of the most striking differences, in comparing the latter with the Chlorococcales, is the complete absence of differentiated colonial types in the Heterococcales, a feature which corresponds to their absence among Heterochloridales.

Several of the Heterococcales exhibit perculiarities in the structure of the cell-wall[2] which is probably in all Heterokontae far richer in pectic substances than is the rule among Isokontae. In *Pseudotetraëdron*, *Centritractus* (fig. 127, A), a few species of *Characiopsis*[3], and the marine *Halosphaera* the cell-wall is composed of two, usually overlapping, pieces, whilst in *Chlorobotrys* Bohlin[4] has recorded the formation of flat cylindrical endogenous cysts (cf. fig. 122, C) having a bivalved silicified membrane; similar cysts occur in *Pseudotetraëdron*, *Halosphaera*, and *Meringosphaera*. In the last two, as well as in *Chlorobotrys* and *Botrydiopsis*, the wall of the ordinary cells is silicified. It is not improbable that the bipartite character of the wall may be more widely spread among Heterococcales, since it is evidently a common characteristic in the Heterokontae (cf. below).

The multinucleate habit among Chlorococcales finds its parallel in *Ophiocytium* among the zoosporic Heterococcales. This is an abundant freshwater form having the shape of a more or less elongated cylinder, usually somewhat curved and sometimes even spirally wound, whilst one or both ends are provided with a stalk-like process by means of which attachment is effected in the epiphytic species (cf. fig. 130). Here again the membrane is composed of two pieces, which are however of very unequal size (as in *Characiopsis*). By treatment with potash one can distinguish a small structureless lid and an elongated basal portion (fig. 130, K) composed of a series of strata, each resembling a long thimble with a strongly thickened rim; by apposition of successive strata both thickening of the wall and growth in length of the whole cell are brought about[5]. Reproduction is effected by zoospores or aplanospores, which are liberated by detachment of the lid.

[1] Pascher (loc. cit. p. 490) draws attention to the close similarity between this genus and *Botrydiopsis*, and he is evidently even inclined to advocate an inclusion of the latter in *Halosphaera*.

[2] cf. Pascher, 1921, p. 241.

[3] cf. Printz, Vidensk. Selsk. Skrift., Mat.-nat. Kl., No. 6, 1913, p. 44; the figures of Carter (New Phytol. XVIII, 1919, pp. 180, 182) however show nothing of the kind.

[4] Bih. K. Sv. Vet.-Akad. Handl. XXVII, 1901, Afd. 3, No. 4, p. 36.

[5] cf. Bohlin, Bih. K. Sv. Vet.-Akad. Handl. XXIII, 1897, Afd. 3, No. 3, p. 31.

Only one group of filamentous forms, the Heterotrichales, is at present known among Heterokontae. They include the exceedingly common *Tribonema* (*Conferva*), which superficially resembles some of the species of *Microspora* (p. 162), and the two genera were indeed long confused. In the unbranched threads of *Tribonema* the uniform cells have a wall composed of two overlapping portions, so that the filaments tend to dissociate into H-shaped pieces (cf. fig. 131), as in *Microspora*; this is, however, the only real resemblance, since all the other characteristics of *Tribonema* are typically Heterokontan. Bohlin[1] showed that the two halves of a *Tribonema*-cell are directly comparable with those of an *Ophiocytium*-individual, but in the former case they are equal and the strata are devoid of the thickened rim (cf. fig. 131, G). The Heterotrichales also include the branched *Monocilia*[2] (= *Heterococcus* Chodat) which is not yet recorded in this country; the short cylindrical or barrel-shaped cells are all alike and seem to have a simple wall (fig. 2, I), but the remaining features are typically Heterokontan.

Zoospores (fig. 122, D) have been noted in all the members of Heterotrichales, while aplanospores are known in *Tribonema* and *Monocilia*. Gametes have been recorded both in *Tribonema* and *Bumilleria*; in the former, according to Scherffel,[3] an active male gamete fuses with a female which has come to rest. This is however the only instance of sexual differentiation that has become known in Heterokontae, where sexual reproduction would altogether appear to be of rare occurrence.

The interesting mud-Alga *Botrydium* (fig. 132) is a probable representative of the siphoneous tendency among Heterokontae, but its position here must remain doubtful until the question of the presence of pyrenoid-like bodies, recorded by Klebs[4] in young individuals, is cleared up. Apart from this, there is nothing that speaks against a Heterokontan affinity, even should the uniciliate character of the zoospores be confirmed (cf. footnote on p. 296). At present *Botrydium* stands alone as a Heterokontan siphoneous type, the reference of *Vaucheria* to this class being no longer entertained (cf. p. 289). On the other hand Lagerheim's *Harpochytrium*[5], a colourless epiphyte on freshwater Algae, is suspected of being a specialised member of this series.

[1] cf. Bohlin, Bih. K. Sv. Vet.-Akad. Handl. XXIII, 1897, Afd. 3, No. 3, p. 31.
[2] Gerneck, 1907, p. 263; cf. also Chodat, 1913, p. 177.
[3] Bot. Zeit. LIX, 1901, p. 149.
[4] Klebs, 1896, p. 224.
[5] Lagerheim, Hedwigia, XXIX, 1890, p. 142.

The following classification of Heterokontae is essentially based on the scheme proposed by Pascher[1], but has been slightly modified to bring out the parallelism with the arrangement of Isokontae adopted in this book:

A. *Heterochloridales*, including the motile types or their obvious derivatives.

I. *Chloramoebales* in which the dominant phase in the life-cycle is a motile one.

II. *Mischococcales* in which the dominant phase is a sedentary one and the individuals are united to form dendroid colonies.

III. *Heterocapsales* in which the dominant phase is also sedentary, the individuals being embedded in palmelloid colonies.

B. *Heterococcales*, including the unicellular sedentary "chlorococcoid" types.

C. *Heterotrichales*, including the filamentous members.

D. *Heterosiphonales*, including the siphoneous type *Botrydium*.

The following key[2] should facilitate the determination of the British genera:

A. Unicellular or colonial, aquatic, not macroscopic, nor inhabiting damp mud

a. Non-colonial, individuals epiphytic, stalked

1. Cells with a very thin stalk and one chloropl. *Stipitococcus*
2. Cells with a thick stalk and several or many chloropl. *Characiopsis*

b. Colonial, consisting of few or many cells, embedded in or united by mucilage

1. Free-floating, planktonic

* Cells pyriform, oblong, or globose, arranged in radiating series within structureless mucilage *Askenasyella*

** Cells ellipsoid or obovate arranged peripherally within tough structureless, often orange-coloured, mucus *Botryococcus*

*** Cells ovoid or oblong, united in groups of four by short mucous bands *Stichogloea*

2. Epiphytic, cells united by mucilage-tubes to form dendroid colonies *Mischococcus*

c. Individuals free-floating (rarely attached), usually spherical, sometimes forming indefinite colonies

1. Cell-wall apparently of a single piece, cells spherical

[1] Hedwigia, LIII, 1912, p. 6. Excellent systematic accounts of the Heterokontae have been given by Heering (Jahrb. Hamburg. Wiss. Anstalt. XXIII, 3 Beiheft, 1905, p. 90) and later by Pascher (1925).

[2] Owing to our imperfect knowledge of many of the genera of Heterokontae and since relatively few of them are recorded for the British Isles, it has not been deemed feasible to arrange this key according to the natural scheme of classification given above.

* Cells aggregated within hyaline mucilage to form families of 2–16, no zoospores *Chlorobotrys*

** Cells solitary, reprod. by zoosp. *Botrydiopsis*

2. Cell-wall of two equal pieces, each prolonged into a long spine *Centritractus*

3. Individuals free-floating or attached, elongated and often curved, wall of two unequal pieces, multinucleate *Ophiocytium*

B. Filamentous, aquatic or terrestrial

a. Cell-walls firm, splitting into H-pieces *Tribonema*

b. Cell-walls hyaline, H-pieces not evident, filaments short *Bumilleria*

C. Coenocytic, macroscopic, growing on damp mud, body composed of overground green vesicle and subterranean rhizoid-portion *Botrydium*

GROUP 1. HETEROCHLORIDALES

Series I. CHLORAMOEBALES

There is only one British genus, which is of very uncertain systematic position and possibly belongs to Chrysomonadales (cf. Pascher, 1925, p. 27), viz.

Stipitococcus W. & G. S. West, 1898[1]. Cells very minute gregarious, epiphytic, enclosed within an envelope which is attached by an extremely fine elongated stalk to various filamentous Algae; envelope at first (?) ovoid and apiculate, then campanulate, with a rounded base and an irregularly expanded apex. Chloropl. single, parietal, pale green, irregular in form; nucleus single in centre of cell. Reprod. by zoosp. with a single long cilium, produced in pairs within the parent-cell and becoming attached by the end of the cilium which forms the stalk(?) of the new individual.

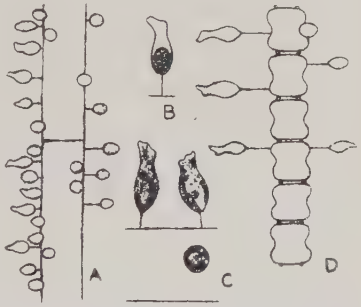

Fig. 123. *Stipitococcus urceolatus* W. & G. S. West; A–C, epiphytic on a filament of *Mougeotia*, from Oughtershaw Tarn, W. Yorks; A, ×500; B and C, ×780; D, epiphytic on *Sphaerozosma excavatum*, from Harris, Outer Hebrides (×500).

S. urceolatus W. & G. S. West (fig. 123) is known from W. Yorks and N.W. Scotland as an epiphyte on *Mougeotia* and *Sphaerozosma*;

[1] W. and G. S. West, Journ. of Bot. xxxvi, 1898, p. 336.

cells 3–4·2 br.; 6·5–10·5 l. A second species has been described from Germany[1]. A close ally is Gobi's *Peroniella*[2], but both genera are very imperfectly known. The published accounts of *Stipitococcus* leave the question as to the presence or absence of a cell-membrane vague, but the protoplast is probably naked and metabolic.

Series II. MISCHOCOCCALES

This at present includes only the genus

Mischococcus Naegeli, 1849[3]. Cells globular, situated at the extremities of thick tubular mucilage-stalks and united to form small branched colonies. Chloropl. 1–4 per cell. Reprod. by 1-ciliate[4] zoosp. with two chloropl., formed singly in the terminal cells and stated sometimes to function as gametes. On coming

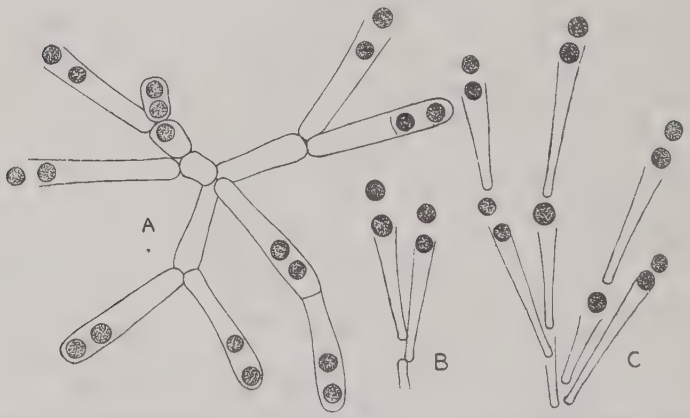

Fig. 124. *Mischococcus confervicola* Naeg. A, from Cam Fell, W. Yorks; B and C, from Ruislip Reservoir, Middlesex (× 500).

to rest the zoosp. rounds off and secretes a short mucilage-tube; this is followed by (mainly transv.) cell-div., the products becoming separated by further mucilage-secretion; sooner or later branching is initiated, the two cells formed by a division secreting mucilage-tubes in different directions. The zygosp. is stated[5] to divide in two directions in one plane forming an epi-

[1] Schmidle, Hedwigia, XLI, 1902, p. 151.

[2] Gobi, Script. Bot. Hort. Univ. Imp. Petropolitanae, I, 1886, p. 244; Serbinow, ibid. XXIII, 1906, p. 91.

[3] Naegeli, 1849, p. 80; Borzi, Stud. Algol. II, 1895, p. 121, and Malpighia, II, 1888, p. 133; Pascher, 1925, p. 33.

[4] West (1916 *a*, p. 404) speaks of "unequal cilia."

[5] cf. Oltmanns, 1922, p. 26.

phytic cushion, all the cells of which are situated on short broad mucilage-stalks.

M. confervicola Naeg. (fig. 124) is a rather uncommon epiphyte on various filamentous Algae in small ponds and ditches, or more rarely in peaty pools; cells 3·5–5·5 br.

Series III. HETEROCAPSALES

Botryococcus Kützing, 1849[1] (incl. *Ineffigiata* W. & G. S. West, 1897, emend. 1903; *Botryomonas* Schmidle, 1899; *Botryodictyon* Lemmermann, 1903). Colonies free-floating, of very varied shape, composed of a number of more or less spherical cell-aggregates embedded within a tough (sometimes orange-coloured) mucous envelope which is folded, wrinkled, and frequently drawn out into irregular lobes, processes, or spines; the smaller colonies sometimes united by more or less rigid prolongations of the envelope into much larger ones. Cells ellipsoid or obovate, arranged peripherally within each aggregate about a central mucilaginous region (cf. also below); chloropl. single, cup-shaped or discoid, containing a naked pyrenoid-like body (fig. 125, C, D) and occasionally with small granules of starch (? Chodat, loc. cit. p. 338); large quantities of oil often present. The cells can at times be squeezed out of the envelopes which are so firm that they retain their shape. Multiplication of cells by longit. div. only, whereby increase of cell-aggregates is brought about, these later becoming separated by the development of

Fig. 125. *Botryococcus Braunii* Kütz., from Harris, Outer Hebrides. A, outline of colony; B, smaller colony; C, part of single family in section; D, colony, from which many cells have been pressed out. (All ×450.)

[1] Chodat, Journ. de Bot. x, 1896, p. 333; West and West, 1897, p. 503; West and West, 1903, p. 80; Carlson, Bot. stud. till. Kjellman, Upsala, 1906, p. 141; Smith, 1920, p. 83; Pascher, 1925, p. 86.

elongated processes of the envelope; vegetative propagation by fragmentation of the older colonies. Production of swarmers doubtful. Pascher (1925, p. 39) refers this genus to the Heterococcales.

Botryococcus Braunii Kütz. (fig. 125) is a very widely distributed Alga, being found in ditches, bogs, tanks, water-butts, and as a plankton-form in large ponds and lakes; cells 3·4–9 br.; 5·7–10·5 l.; diam. of single aggregates 21–56, of colonies 46–350 (in the plankton up to 1½ mm.). When it occurs in quantity the cells develop abundant oil, which in the late summer becomes brick-red owing to a pigment dissolved in it; the oil sometimes escapes from the cells and adheres to the aggregates and processes of the enveloping mucus. Although frequently investigated, the structure and reproduction of this widespread form are incompletely known, and the accounts of the same investigator published at intervals in no way agree with one another. This is in great part due to the fact that the tough and highly irregular mucilage-envelope obscures to a very large extent the cell-structure, so that the individual aggregates are almost indecipherable. Each cell appears to be located within a funnel-shaped and often stratified mucilage-cup whose base is prolonged into a thick stalk which extends to the centre of the aggregate; this structure is however only readily recognisable in young stages. The origin of the envelope is not clearly established. It appears that in some cases the cells lie at the periphery of the mucilage whilst in other cases the latter forms a definite superficial layer. Some of the specially opaque stages were described by W. & G. S. West in 1897 under the appropriate name of *Ineffigiata neglecta*, whose identity with *B. Braunii* was only later established. The reference of the Alga to Heterokontae is not altogether certain and, if the reported presence of starch and of a "pyrenoid" is correct, it would even seem very doubtful. Carlson (loc. cit. p. 143) records the presence of short "pseudocilia" arising in a tuft from the outer end of the cell.

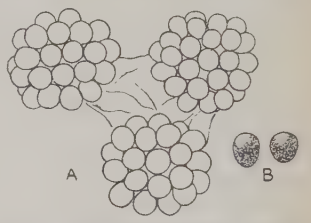

Fig. 126. *Botryococcus sudeticus* Lemm., from the New Forest, Hants. A, small colony; B, two isolated cells (×450).

The three other sp. known from the Brit. Isles are rarer. *B. sudeticus* Lemm. (fig. 126)[1], in which the gelatinous membrane is more delicate, has been recorded from various localities, whilst *B. protuberans* W. & G. S. West is known from the plankton of Loch Fadaghoda, Lewis, and is distinguished by prominent projection of the cells from the mucus in which they are embedded (West and West, 1905, p. 507).

[1] Chodat (cf. Bull. Soc. Bot. Genève, VII, 1915, p. 193, and XIII, 1921, p. 93) and Pascher (1925, p. 91) place this species in a distinct genus (*Botryosphaera*).

Askenasyella Schmidle, 1902[1] (incl. *Actinobotrys* W. & G. S. West, 1905[2]). Cells pyriform, oblong, ellipsoid, or globose, more or less densely arranged in series radiating from the centre of a globular or somewhat irregular mass of structureless mucilage to form free-floating colonies. Chloropl. single, parietal, generally with lobed margins. Zoosp. with a single cilium recorded.

A. conferta W. & G. S. West (*Actinobotrys confertus* W. & G. S. West) (fig. 127, B, C) has been found in the plankton of various Scotch and Irish lakes, as well as in some of the bogs of Sutherland. The cells (4·5–5·8 br.; 6–8·7 l.) are rather densely crowded to form more or less globular colonies and generally show a diminution in size from the centre outwards. Lemmermann[3] and Pascher (1925, p. 84) refer *Actinobotrys confertus* to *Oodesmus* (=*Stichogloea*), but a comparison of the various figures hardly supports this.

Stichogloea Chodat, 1897[4] (incl. *Oodesmus* Schmidle, 1902[5]). Cells small, oblong or ovoid, united by short mucilage-strands or embedded within a mucilaginous membrane to form free-floating groups of fours, more or less disposed in one plane; colonies of 8 or sometimes of 16 cells also observed. Cell-wall firm and sometimes thickened; chloropl. one or two per cell, parietal, olive-green or brownish. Multipl. by fission of colony after cell-division.

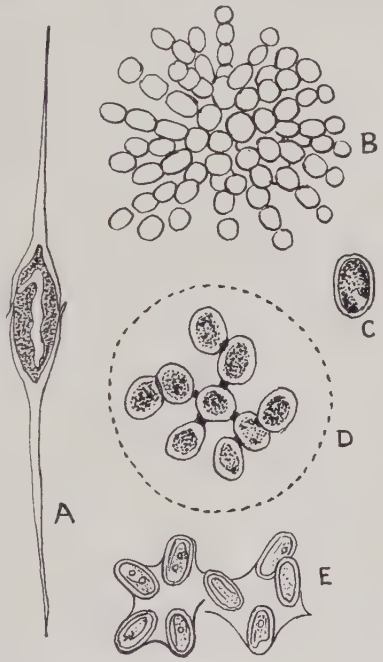

Fig. 127. A, *Centritractus belonophorus* (Schmidle) Lemm. (after Schmidle). B and C, *Askenasyella conferta* W. & G. S. West (after West); B, colony (×520); C, single cell (×1000). D, *Stichogloea Doederleinii* (Schmidle) (after Lemmermann, ×776). E, *S. olivacea* Chod. (after Chodat).

The two sp. of this genus are very imperfectly known, and it is not impossible that with further study they may be relegated to another

[1] Schmidle, Hedwigia, XLI, 1902, p. 154.
[2] West and West, 1905, p. 508; West and West, 1906, p. 108.
[3] Archiv f. Hydrobiol. u. Planktonk. V, 1910, p. 327.
[4] Chodat, 1897, p. 302.
[5] Schmidle, Hedwigia, XLI, 1902, p. 162.

class[1]; it is possible too that they would find a more suitable place in the Heterococcales. *S. olivacea* Chod. (cells 9–15 l.) (fig. 127, E) is known from the plankton of certain Scotch lakes, whilst *S. Doederleinii* (Schmidle) (*Oodesmus Doederleinii* Schmidle; cells 6 br.; 8 l.) (fig. 127, D) has been reported by Lemmermann[2] in the plankton of Loch Doon, Ayrshire. Pascher regards these two species as synonymous and would also include with them *Askenasyella conferta*.

GROUP 2. HETEROCOCCALES

Family 1. CHLOROBOTRYDACEAE

This includes a number of free-floating unicellular forms with firm walls and from two to many parietal chloroplasts in each cell. Reproduction is effected by zoospores or aplanospores, by special bivalved cysts, and (in *Botrydiopsis*) by isogametes.

Chlorobotrys Bohlin, 1901[3]. Cells globose, subglobose, or broadly ovoid, solitary or more commonly in families of 2, 4, 8, or 16 surrounded by a wide hyaline homogeneous mucilage-envelope; cell-walls firm, smooth, of some thickness and often

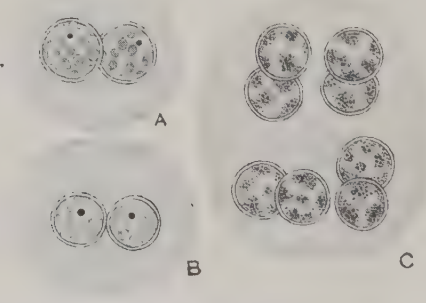

Fig. 128. *Chlorobotrys regularis* (West) Bohlin, from Tremethick Moor, Cornwall (×450).

prominently silicified. Chloropl. 3–30 in number, discoid, parietal, but the pigment sometimes more or less diffuse; a prominent red pigment-spot is commonly found in each cell. Reprod. by div. of protoplasts in two or three directions, with formation of colonies which, when consisting of 4–16 cells, are often very

[1] cf. Pascher, Hedwigia, LIII, 1912, p. 13; Pascher, 1925, p. 84.
[2] W. and G. S. West, Journ. Linn. Soc., Bot. XXXV, 1903, p. 532.
[3] Bohlin, Bih. K. Sv. Vet.-Ak. Handl. XXVII, 1901, Afd. III, No. 4, p. 34; West and West, 1903, p. 78; Smith, 1920, p. 82.

symmetrical; later these cells fall apart[1]. Bivalved silicified cysts having the shape of flat cylinders are formed from the contents of ordinary cells, on germination producing a few aplanosp. which are liberated by separation of the valves (fig. 122, C).

The mode of division and the method of cyst-formation require further study. Of the two sp., *C. regularis* (West) Bohlin (*Chlorococcum regulare* West) is widely distributed and often abundant in the *Sphagnum*-bogs of the Brit. Isles; cells 12–19, families with investment 34–90 br. (fig. 128). *C. limneticus* Smith, with ovoid cells (5–6 × 6–8) having only 3–4 chloropl., is recorded by Pearsall[2] from the plankton of various lakes of the Lake District.

Botrydiopsis Borzi, 1889[3]. Cells rather large, spherical, isolated, free-floating, with a delicate and colourless wall, which is sometimes slightly silicified and composed of two pieces; there is a rather large central nucleus, and numerous parietal discoid chloropl. Reprod. by typical Heterokontan zoosp. or aplanosp., formed in large numbers in the cells; those producing zoosp. are more or less ovoid. In some cases the aplanosp. become thick-walled resting cells with deep red oily contents and on germination produce isogametes with almost equal cilia; the spherical zygosp. gives rise to ordinary vegetative cells. Bivalved cysts with a membrane composed of two unequal halves recorded by Pascher[4].

The only known sp., *B. arrhiza* Borzi (fig. 122, B), has been recorded by G. S. West from Berkswell, near Birmingham (Grove, 1920, p. 53); cells 30–40 br.

Centritractus Lemmermann, 1900[5]. Cells solitary, cylindrical, with conical extremities prolonged into a long pointed spine; wall coarse, composed of two overlapping pieces. Chloropl. two or more, parietal, sometimes reticulate; cells 1-nucleate. Reprod. by transv. div.

The only sp., *C. belonophorus* (Schmidle) Lemm. (*Schroederia belonophora* Schmidle (fig. 127, A)), is a rare plankton Alga which has been recorded by G. S. West from Berkswell, near Birmingham (Grove, 1920, p. 53).

[1] Poulton (Bull. Soc. Bot. Genève, XVII, 1925, p. 13) records zoospores in a form described as *C. stellata* Chod. which is as yet only known in cultures, but the assignation of this Alga to the genus *Chlorobotrys* appears doubtful.

[2] Journ. Linn. Soc., Bot. XLVII, 1925, p. 72.

[3] Borzi, Stud. Algol. II, 1895, p. 169; Chodat, 1913, p. 174; Poulton, loc. cit. p. 20. With reference to the possible relation of this genus to *Halosphaera*, cf. p. 298.

[4] Ber. Deutsch. Bot. Ges. XXXIII, 1915, p. 490.

[5] Lemmermann, ibid. XVIII, 1900, p. 274.

Family 2. CHLOROTHECIACEAE

A family of unicellular epiphytes reproducing by zoospores or aplanospores.

Characiopsis Borzi, 1895[1]. Cells epiphytic, solitary or gregarious, rounded, ellipsoid, or ovoid, sometimes acuminate, with a firm wall and a short thick basal stalk terminating in an adhesive disc. Chloropl. several or many, parietal, or filling the greater part of the cell-cavity; cells probably at first uni-, later multi-nucleate. Reprod. by zoosp., formed 4–16 per cell and liberated by rupture or dissolution of the upper part of the wall of the parent-cell; aplanosp. giving rise to 2–4 gametes also known; zygosp. on germination producing two zoosp.

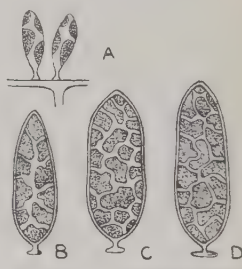

Fig. 129. A, *Characiopsis minuta* (A. Br.) Borzi, from near Penzance, Cornwall. B–D, *C. turgida* W. & G. S. West, from Keighley Moor, W. Yorks (×500).

Most of the sp. were at one time described as sp. of *Characium*. Of the four Brit. sp., *C. minuta* (A. Br.) Borzi (fig. 129, A) is the most frequent; cells 5·5 br. and 17–18 l. The largest sp. are *C. turgida* W. & G. S. West (cells 11·5–16 br.; 36–46 l.) (fig. 129, B–D) and *C. Naegelii* (A. Br.) Lemm., the latter with oval, elliptical, or subspherical cells (6–28 br.; 16–50 l.) with a broadly rounded apex.

Characium cylindricum Lambert (cells up to 240 l.), recorded by Griffiths[2] on Rotifers, is likely to be a sp. of *Characiopsis*.

Family 3. OPHIOCYTIACEAE

The only genus is

Ophiocytium Naegeli, 1849[3] (incl. *Sciadium* A. Braun, 1855). Individuals free or attached, commonly solitary but sometimes colonial (fig. 130, J), mostly many times longer than their diam. and usually curved or spirally contorted, the two ends being similar (blunt or spined) or one end more or less distinctly swollen and the other produced into a stalk or spine; cell-wall consisting of a homogeneous lid fitted to the apex of a long tube composed of successive layers of pectose compounds (cf. p. 298 and fig. 130, K). Cells, when mature, multinucleate, with a

[1] Borzi, Stud. Algol. II, 1895, p. 151; Lemmermann, Abh. Nat. Ver. Bremen, XXIII, 1914, p. 249; Carter, New Phytol. XVIII, 1919, p. 177.

[2] Griffiths, 1923, p. 190.

[3] Naegeli, 1849, p. 87; Braun, 1855, p. 48; Bohlin, Bih. K. Sv. Vet.-Ak. Handl. XXIII, 1897, Afd. 3, No. 3, p. 31; Lemmermann, Hedwigia, XXXVIII, 1899, p. 20; Pascher, 1925, p. 72.

number of large parietal somewhat H-shaped chloropl. (fig. 130, A). Reprod. by ovoid 2-ciliate zoosp., eight formed per cell, or by ellipsoidal aplanosp.[1]; liberation by detachment of the lid (fig. 130, C). In the attached sp. the zoosp. usually settle down at the rim of the empty parent-individual and there grow into adult cells; if this is repeated, dendroid colonies result. Gametes not observed.

This genus appears closely related to *Tribonema* (cf. Bohlin, loc. cit.). The best systematic account is that given by Heering (cf. p. 300); see

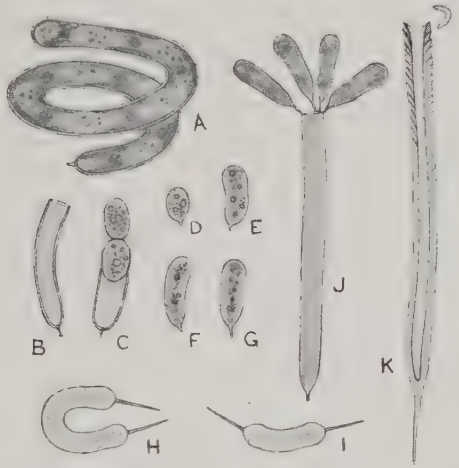

Fig. 130. A, *Ophiocytium majus* Naeg., from Bowness, Westmorland. B–G, *O. cochleare* (Eichw.) A. Br., from same locality. H and I, *O. bicuspidatum* (Borge) Lemm. forma *longispina* Lemm., from Pilmoor, N. Yorks. J, *O. Arbuscula* (A. Br.) Rabenh., from Mitcham Common, Surrey. (All × 450.) K, *O. graciliceps* (A. Br.) Rabenh., after treatment with potash (after Bohlin, × 570).

also Lemmermann, loc. cit. Six sp. are known to occur in the Brit. Isles, several of which are widely distributed, especially in small ponds and pools which are poorly aerated. *O. Arbuscula* (A. Br.) Rabenh. (*Sciadium Arbuscula* A. Br.) is an attached sp. often developing characteristic branch-systems (fig. 130, J; cells 3–8 br.). The largest sp. is *O. majus* Naeg. (fig. 130, A), with cells up to 17 μ br. *O. cochleare* (Eichw.) A. Br. (fig. 130, B–G; cells 5–8 br.), *O. capitatum* Wolle (spinous at either end, cells 2·7–10 br.), *O. bicuspidatum* (Borge) Lemm. (fig. 130, H and I; cells 12–15 br.), and *O. parvulum* (Perty) A. Br. (blunt at both ends, cells 3–9 br.) are also frequent.

[1] According to Pascher (1921, p. 242) these spores have a bivalved wall composed of two unequal pieces.

GROUP 3. HETEROTRICHALES

This comprises the filamentous Heterokontae which may at present all be grouped in the

Family TRIBONEMACEAE

Tribonema Derbès & Solier, 1856[1] (*Conferva* in the sense used by Lagerheim, 1888). Filaments unbranched, composed of uniform cylindrical or slightly barrel-shaped cells, with walls which are often of considerable thickness and consist of two overlapping pieces built up of successive strata of pectic substances (fig. 131, G); filaments readily breaking into H-shaped pieces, composed of a septum and the cylindrical halves of the adjacent cells on either side. Cells with one nucleus (sometimes two) and a number of parietal chloropl. which are occasionally few and irregular in shape, but more often numerous and discoid. Asex. reprod. by formation of akinetes and of 1–5 typical zoosp. (fig. 131, C) or globular or ellipsoidal aplanosp.[2] (fig. 131, I) in any cell; liberation by breaking of the filament into H-shaped pieces. Young filaments originating from zoosp. at first attached by a stalk-like base (fig. 131, F), those formed from aplanosp. free-floating *ab initio*. Sex reprod. by fusion of morphologically similar gametes, provided with a reddish-brown stigma, one of which comes to rest and rounds off before the other active gamete fuses with it; zygosp. spherical.

The generic name *Conferva* goes back to the time of Pliny, and Linnaeus included under it most of the branching as well as the simple filamentous Algae then known. Hazen (loc. cit.) first pointed out that "there is no warrant whatever for employing the name *Conferva* to designate the genus recognised under that name in Lagerheim's revision, for there is no evidence that these species were ever collected by Linnaeus, and certainly none of them was distinguished by him from other simple filamentous forms. For Lagerheim's group of species the adoption of a generic name based on a recognisable species as a type is essential. The earliest such name in the present case is *Tribonema* Derbès and Solier, 1856. This genus was based on a single species, *C. bombycina*, and in the diagnosis, for the first time in the history of the species, explicit mention was made of the most essential character, namely the form of the chromatophores." These are briefly the grounds for the abandonment of the name *Conferva* and the adoption of *Tribonema*.

[1] Lagerheim, Flora, LXXII, 1889, p. 194; Klebs, 1896, p. 346; Bohlin, loc. cit. p. 3 et seq.; Hazen, 1902, p. 181; Poulton, loc. cit. p. 59.

[2] According to Pascher (1921, p. 242) these spores have a bivalved wall.

Of the six Brit. sp., *T. bombycinum* (Ag.) Derb. & Sol. (= *Conferva bombycina* Ag. (fig. 131, A–G)) is very widely distributed in varied habitats, being also occasionally found in cultivated soils; like many other Heterokontae it favours shaded pools or those which are grass-grown at the margin; its cells are 8–15 br., but a small form with cells only 5–6·5 br. (f. *minor* (Wille) G. S. West (fig. 131, H and I)) is also

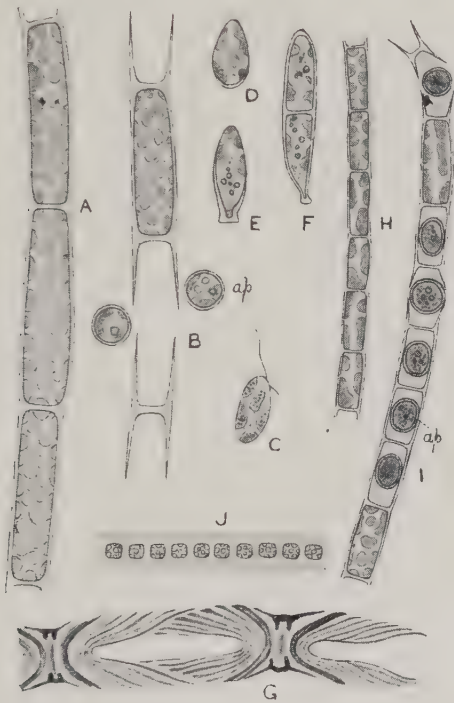

Fig. 131. A–G, *Tribonema bombycinum* (Ag.) Derbès & Sol.; A, from Shipley, W. Yorks; B, showing aplanospores (*ap*), from Senens, Cornwall; C, zoospore, and D–F, young plants, from Senens, Cornwall (all ×450); G, after treatment with potash (after Bohlin, ×570). H and I, *T. bombycinum* forma *minor* (Wille) G. S. West; H, from Shipley, W. Yorks; I, showing aplanospores (*ap*), from near St Just, Cornwall (×450). J, *Bumilleria pumila* W. & G. S. West, from near Senens, Cornwall (×450).

very common. *T. affine* (Kütz.) G. S. West (=*C. affinis* Kütz.) has very narrow (5–5·4 br.) and elongated cells with few irregular chloropl. and the apical cell is apiculate. A much rarer sp. is *T. obsoletum* G. S. West (=*C. obsoleta* W. & G. S. West, 1903, p. 77), with cells 19–21 br. and very small and numerous chloropl. which are densely crowded.

Bumilleria Borzi, 1895[1]. Filaments unbranched, composed of uniform oblong, barrel-shaped, or almost quadratic cells, often loosely connected and with a homogeneous wall composed of pectic substances; the latter may sometimes form a distinct mucous cylinder in which the cells appear embedded and gives indication of H-shaped structure only in some sp. Cells with 1–2 nuclei and 2–12 parietal pulvinate chloropl. (fig. 122, A). Reprod. by fragmentation and by 1-ciliate zoosp. of which 2–4 are formed in each cell; also by aplanosp. in one sp. Sex. reprod. doubtful. Resting akinetes readily formed on exposure to drought.

The sp. of this genus are in part very incompletely known and one may feel considerable doubt whether they form a homogeneous group. Two are recorded for Gt Britain. In *B. exilis* Klebs (cells 4·5 br.; 10–15 l.) (fig. 122, A), which is an abundant soil-Alga (Bristol, 1920, p. 78), but has also been found in ponds, the H-shaped structure is apparent and reprod. by fragmentation is common; this sp. stands very close to *Tribonema*. *B. pumila* W. & G. S. West (cells 4·8–5·7 br.; 5–6 l.) (fig. 131, J), on the other hand, has quadrate cells showing no signs of H-structure, the cells being embedded in a mucilage-cylinder (West and West, 1903, p. 77); it may be doubted whether this sp. belongs to the same genus as the other (cf. Heering, loc. cit. p. 142, and Pascher, 1925, p. 112).

GROUP 4. HETEROSIPHONALES

This includes only the genus

Botrydium Wallroth, 1815[2]. Macroscopic, individuals composed of green pear-shaped or spherical vesicular coenocytes of considerable size, rooted in damp mud by a branched system of colourless rhizoids. The central sap-cavity is continuous throughout the plant and the lining layer of cytoplasm contains numerous nuclei and, in the overground vesicle, numerous peripheral lenticular or fusiform chloropl. more or less evenly distributed in one or more layers; doubtful pyrens. have been observed in young stages. Asex. reprod. by small ovoid 1-ciliate[3] zoosp. with one or two chloropl., formed when the plants are submerged; they arise in very large numbers by div. of the protoplasmic contents of the vesicle and escape through an opening at its

[1] Borzi, Stud. Algol. II, 1895, p. 185; Klebs, 1896, p. 376; Chodat, 1913, p. 180.

[2] Rostafinski and Woronin, Bot. Zeit. XXXV, 1877, p. 649; Klebs, 1896, p. 223.

[3] West (1916 *a*, p. 415) speaks of two unequal cilia, but the evidence for this is not apparent.

apex; if the plants are wet but not submerged, aplanosp. are formed. As a response to drought the protoplasmic contents migrate into the rhizoids and by subdivision form a large number of thick-walled resting cysts which are globose or ellipsoid and either germinate directly or produce zoosp. Gametes unknown.

Botrydium granulatum (L.) Grev. (fig. 132) was long confused with *Protosiphon* (cf. p. 111), and Klebs (loc. cit. p. 169 et seq.) first showed clearly that Rostafinski and Woronin had, in their description of

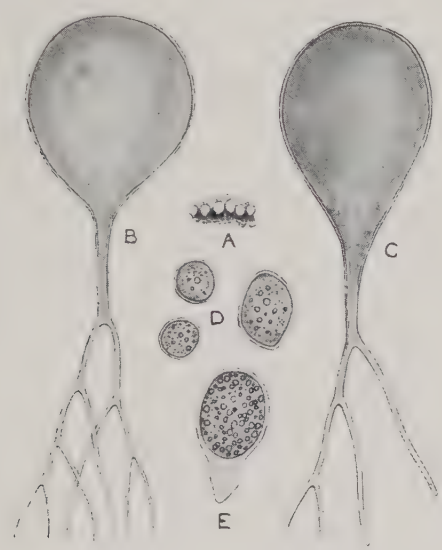

Fig. 132. *Botrydium granulatum* (L.) Grev., from Calverley, W. Yorks. A, nat. size; B and C, ×45; D and E, ×450; D, aplanospores; E, germinating aplanospore.

Botrydium, combined two distinct Algae. It occurs widely distributed over the Brit. Islands, but is very local and the conditions are not often suitable for its appearance above ground. It is found almost exclusively on drying-up mud and sometimes occurs in countless numbers standing out in Mulberry-like masses on mud turned out from a canal or on the drying bottom of a muddy pond. The nature of the mud is immaterial and the Alga is not uncommonly found on chalk mud. The vesicles reach 2·26 mm. in diameter.

CLASS III. CHRYSOPHYCEAE

In the case of Isokontae and Heterokontae the majority of the species known at the present day are possessed of firm cell-walls in the ordinary vegetative condition and altogether show an "algal" construction. The forms placed in Pascher's class Chrysophyceae[1], however, in great part possess naked protoplasts and are essentially "flagellate" in organisation. They exhibit nevertheless such a profound morphological parallelism with Isokontae and Heterokontae that it would be unnatural not to regard them as equivalent or to omit them in a book dealing with Algae; moreover the majority of them are holophytic. The apparent complete absence of sexual reproduction in the members of this class is another indication that, although highly evolved in some respects, they have remained at a relatively low level in others. The Chrysophyceae appear in the main to favour relatively pure waters and seem to attain their greatest development in the cold streams and pools of mountainous regions. Many are characteristic plankton forms.

Like the Heterokontae, the Chrysophyceae are characterised by the possession of chromatophores with a distinctive pigmentation, usually giving the individuals a golden-yellow or brown colour, although in waters rich in organic substance they often assume a green tint. The special coloration is in this case due to varying amounts of one or more accessory pigments (e.g. Gaidukov's phycochrysin[2]) about which as yet little is known. Pyrenoids are lacking (except *Hydrurus*?) and starch is not known to occur. The products of photosynthesis are stored as oil and as colourless highly refractive, usually rounded lumps of a body known as leucosin[3], the latter constituting one of the marked characteristics of the class. Other distinctive peculiarities are afforded by the type of ciliation and by certain features of the cellular envelope when present (cf. the cysts, p. 315). Pascher (1921, p. 236) brings forward evidence supporting an affinity between Heterokontae and Chrysophyceae (similarity in membrane-structure, pigmentation, and assimilatory products, cf. p. 350), for which reason the latter class is considered at this point.

[1] Pascher, 1914, p. 143.

[2] Gaidukov, Ber. Deutsch. Bot. Ges. XVIII, 1900, p. 331.

[3] The chemical composition of leucosin is unknown. It is readily soluble in most reagents and is not affected by iodine. Pascher states that it is found also in Heterokontae (cf. Pascher, 1921, p. 247).

The motile members, classed as Chrysomonadales, fall into three main series differing in their ciliation, but agreeing in other respects. These are:

Chromulinales, with a single cilium.
Hymenomonadales, with two equal cilia (Pascher's Isochrysidales).
Ochromonadales, with two unequal cilia.

The unicellular *Chromulina* is typical of the simpler Chromulinales (Euchromulinaceae) and shows many of the characteristics of the class. The oval or spherical uninucleate cells (fig. 1, C, p. 22) move with the help of a single apical cilium and in many species exhibit a certain amount of metaboly (p. 25); like other motile organisms, they possess one or two contractile vacuoles at the front end and are often provided with an eye-spot. There are one or two[1] (rarely more) large, well-defined parietal chromatophores, more or less brown in colour, and a single mass of leucosin is usually lodged at the posterior end of the cell. Multiplication is effected by longitudinal division, either of the motile individual, or after the latter has come to rest and become enveloped by mucilage. In some species (e.g. *C. Rosanoffii*) extensive mucilage-masses resembling *Palmella*-stages may thus arise, and in *C. mucicola* Lauterborn numerous ciliated cells embedded in diffluent mucilage constitute the normal vegetative condition, swarming here only occurring in connection with reproduction (cf. *Chlamydomonas Kleinii*, p. 65). Such forms lead over to the Chrysocapsales (p. 319). In a few species[2] (e.g. *C. Hokeana* Pascher (fig. 133, C)) there is a slight colonial tendency, the products of division cohering for a short time to form 2–8-celled motile colonies.

The dormant stages of *Chromulina* are constituted by peculiar cysts provided with a silicified wall and formed endogenously. Scherffel[3] has given a detailed description of their development in the case of *C. nebulosa* Cienk. The protoplast secretes near its periphery a hollow silicified membrane provided with a small aperture towards one side (cf. fig. 133, E); the small amount of cytoplasm remaining outside becomes vacuolated and is responsible for the development of the spiral sculpturing on the outer surface of the mature cyst of the species named. Finally the external cytoplasm passes through the pore into the interior of the cyst and the aperture is closed from the inside by the production of a special silicified plug (cf. fig. 133, F), which is usually

[1] Two lateral chromatophores, although not so frequent in *Chromulina*, represent the usual arrangement in the majority of the Chrysomonadales.

[2] Pascher, Ber. Deutsch. Bot. Ges. XXVIII, 1910, p. 339.

[3] Archiv f. Protistenkunde, XXII, 1911, p. 334.

more or less conical. Such cysts are probably characteristic of the Chrysophyceae as a whole and a considerable number are known, though relatively few have been assigned to their appropriate species or genus. The wall of the mature cyst always consists of two pieces which are mostly of very unequal size; in

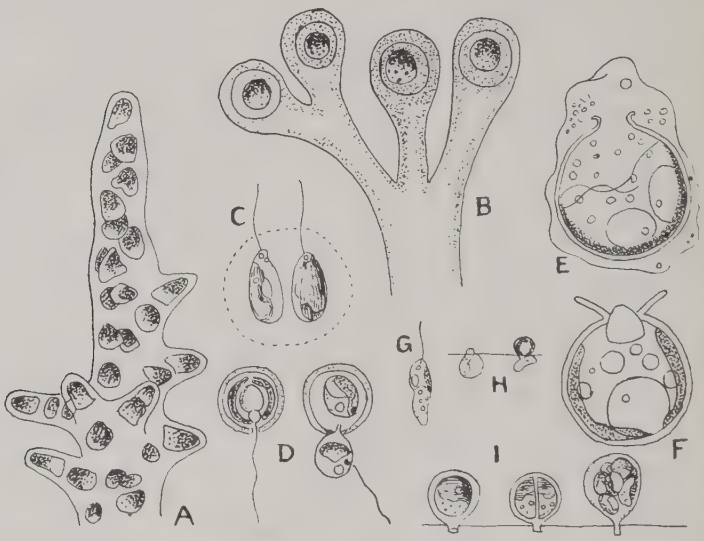

Fig. 133. A–B, *Hydrurus foetidus* (Vill.) Kirchn.; A, small part of a colony (after Berthold, × 470); B, cyst-formation (after Klebs, × 600). C, *Chromulina Hokeana* Pascher (after Pascher). D, *Chrysococcus rufescens* Klebs (after Klebs, × 1000); on the right a stage in division. E, development of a cyst within a species of *Chromulina* (after Pascher). F, fully formed cyst of an *Ochromonas* (after Pascher). G–I, *Chromulina Rosanoffii* (Woron.) Bütschli (after Woronin); G, motile individual (× 540); H, two stages in the formation of the cysts (× 540); I, mature cysts and germination.

a few Chrysophyceae however the two are almost equal (cf. Pascher, 1921, p. 243). Since these cysts contain typical Chrysophycean chromatophores and leucosin, they are readily identified as belonging to members of this class. On germination the cysts give rise to a number of motile individuals which escape through the pore[1].

Chromulina, with its numerous species, is parallel to *Chlamydomonas* and *Chloramoeba*. There is no comparable form among the Hymenomonadales, but *Ochromonas* (Euochromonadaceae)

[1] Regarding the peculiar cysts of *Chromulina Rosanoffii*, see p. 322. Cysts of Chrysomonadales have been recorded in a Diatomaceous earth near Dalmahoy, Edinburgh (see Henderson, Trans. Bot. Soc. Edinburgh, XXIX, 1925, pp. 136, 142).

shows much the same construction and methods of reproduction, the approximately oval cells differing chiefly in the possession of two cilia at the front end, one from 4–6 times the length of the other (fig. 1. D). Both *Chromulina* and *Ochromonas* include a number of colourless species, essentially different only in the absence of chromatophores. In view of the close correspondence between these two genera, too much emphasis should probably not be laid on the varying mode of ciliation in this class (cf. Oltmanns, 1922, p. 21).

The encapsuled type among Chrysomonadales is represented by *Chrysococcus* (fig. 133, D)[1], a *Chromulina* surrounded by a special rigid envelope with a small aperture for the protrusion of the cilium (cf. *Coccomonas*, *Trachelomonas*). In all three series epiphytic types are known, the naked ciliated cells being lodged in relatively commodious and variously shaped envelopes, mostly with a rather wide aperture (cf. fig. 134, E). The mode of attachment to the substratum (usually a filamentous Alga) varies and is especially striking in *Chrysopyxis*[2] (Euchromulinaceae) (fig. 2, A , p. 29), where the lower end of the envelope is continued into two prolongations fitting saddle-wise over the cylindrical thread (generally of Zygnemaceae), the ends being joined by a ring of mucilage encircling the algal filament. The cilia project from the apertures of the envelopes and are usually normally developed, but in *Chrysopyxis* the cilium tends to be replaced by a branched filiform rhizopodium which may be of help in connection with occasional ingestion of solid particles. Such is known to occur also in several of the free-moving members of the class[3].

Not all the motile unicellular Chrysomonadales possess the simple construction above described. In the widely distributed plankton-genus *Mallomonas* (fig. 134, B–D), for example, the usually uniciliate[4] cells, which are of relatively large dimensions and of very varied shape, possess a periplast in which numerous small imbricating silicified scales (cf. fig. 134, C) are deposited. Some or all of these bear delicate hinged, likewise silicified, needles which are commonly of considerable length and doubtless serve to heighten the floating capacity. The cells harbour a number of variously distributed contractile vacuoles, and in

[1] The Coccolithophoridae, frequent members of marine nannoplankton, are probably closely allied forms (cf. Lohman, Arch. f. Protistenkunde, I, 1902, p. 89).

[2] cf. Wille, 1887, p. 473; Iwanoff, Bull. Acad. Imp. Sci. St Pétersbourg, 5 sér. XI, 1899, p. 251.

[3] cf. Scherffel, Bot. Zeit. LIX, 1901, p. 146, and Ber. Deutsch. Bot. Ges. XXII, 1904, p. 439.

[4] Scherffel, loc. cit. 1904, p. 441.

some species the latter are aggregated round a large anterior non-contractile vacuole into which they periodically discharge. Reproduction is effected by longitudinal division and typical cysts are known in many species. A remarkable colonial member of Mallomonadaceae, *Chrysosphaerella*[1], is rare and has so far not been recorded in this country.

Among the Hymenomonadales, however, there are two common colonial plankton-forms, viz. *Syncrypta* (fig. 2, C) and *Synura* (fig. 135), the former with a simple, the latter with a more elaborate periplast. Both form globular colonies of more or less ovoid cells with typical Chrysophycean structure. In *Synura* the periplast is usually beset with numerous short bristles and the cells show a relatively complex vacuolar system resembling that above described for *Mallomonas*. Compared with Volvocales, these colonial forms show a less marked individuality; the movement is irregular, there being no definite anterior end, and the method of reproduction is altogether different, being effected by fission of the mature colonies. In *Synura* Pascher[2] has also recorded propagation by naked swarmers which escape from the bristly periplast and exhibit a simplification of the vacuolar system. This return of the swarmers to a simple type of organisation is a feature of some phylogenetic importance that may be sought for also in other highly organised Chrysomonadales.

Phillips' *Chlorodesmus* (fig. 134, A) is a very striking form closely related to *Synura*. In another colonial Chrysomonad, *Uroglena* (fig. 136, A), the cells of the spherical or ellipsoid aggregates show the structure of an *Ochromonas* (cf. fig. 136, B). All three types of ciliated unicells have thus developed a colonial habit.

Colonies of quite a different stamp are seen in two members of Ochromonadales, viz. *Dinobryon* and *Hyalobryon*; species of the former are abundant plankton-organisms. Non-colonial species of both genera are known, a few of them being epiphytes.

The elongated oval or fusiform cells of *Dinobryon* (fig. 137, A) have a delicate periplast admitting of a certain amount of change of shape; the anterior hyaline end is specially amoeboid and is frequently hollowed out into a kind of mouth serving for the ingestion of small particles. Each cell lies within a wide envelope (usually of cellulose), open in front and more or less pointed at the back end. Like that of *Chrysopyxis*, this envelope consists, according to Pascher (1921, p. 237), of successive thimble-like

[1] Lauterborn, Zool. Anzeiger, XIX, 1896, p. 16, and Zeitschr. f. Wiss. Zool. LXV, 1899, p. 381.

[2] Archiv f. Protistenkunde, XXV, 1912, p. 156.

segments (see fig. 136, F)[1] fitted into one another (cf. Heterokontae, p. 298). In *Hyalobryon* (fig. 136, E, G) the projecting ends of these segments are visible without further treatment. The base of the protoplast in both genera is extended as a contractile thread which is attached to the base of the envelope, commonly a little towards one side (cf. fig. 137, A), and by its means the cells are not only able to withdraw somewhat into the envelope, but can also travel along its side till they reach the aperture.

Reproduction is effected by the usual longitudinal division and, in the non-colonial species, the one daughter-cell, as in *Chrysococcus*, etc., escapes and forms a new envelope. Colonies arise by one (fig. 137, A) or both (fig. 137, C) of the new cells moving up to the aperture of the parent-envelope and settling down there; in this way variously branched aggregates are produced. In the formation of the envelope a small funnel-shaped piece first arises at the base and thereupon the protoplast rotates upon its axis, describing a funnel-shaped course, and slowly secretes the remainder of the envelope[2].

The *Palmella*-stages, that are not exactly rare among the Chrysomonadales, no doubt indicate the method of evolution of the Chrysocapsales, corresponding to the Tetrasporales among Isokontae. Such are *Chrysocapsa* (fig. 138), *Phaeosphaera* (fig. 139), and the highly differentiated *Hydrurus* (fig. 140) which far exceeds in its marked division of labour any of the palmelloid forms found in other classes and may in some respects be ranked as high as a *Draparnaldia*.

In the British Islands no representatives of this class corresponding to the Chlorococcales have become known, but Pascher[3] has described a number of Chrysosphaerales, e.g. *Chrysosphaera* (fig. 2, F), with motionless spherical or ellipsoidal cells reproducing by *Chromulina*-like swarmers (fig. 2, G), and evidently parallel to *Chlorococcum* or *Botrydiopsis*. A more striking development is that seen in the Chrysotrichales, comprising *Phacothamnion* (fig. 141) and other interesting filamentous members, as yet unknown in this country. Examples are Pascher's *Nematochrysis* (= *Chrysothrix*)[4] which is unbranched and has Ochromonad zoospores, and Conrad's *Thallochrysis*[5]

[1] These can be demonstrated in certain species (e.g. *D. Utriculus*) by boiling with potash and staining with Congo Red.

[2] Klebs, Zeitschr. wiss. Zool. LV, 1893, p. 399; Pascher, 1913, p. 64.

[3] Pascher, 1914, p. 159; and Archiv f. Protistenk. LII, 1925, p. 533.

[4] Pascher, 1914, p. 159; Ber. Deutsch. Bot. Ges. XXXII, 1914, p. 430; loc. cit. 1925, p. 511.

[5] Conrad, Bull. Sci. Acad. Roy. Belgique, 1920, p. 180; Pascher, loc. cit. 1925, p. 515.

which is branched and has *Chromulina*-like swarmers; typical siliceous cysts are recorded in the last-named genus. With the recognition of the algal types mentioned in this paragraph the concept of a parallel evolution of Isokontae, Heterokontae, Chrysophyceae, etc. has been very materially strengthened. It is to be hoped that the many forms recorded from the continent will not remain long undiscovered in this country.

In recent years, largely as a result of the investigations of Pascher[1], a considerable number of normally rhizopodial representatives of Chrysophyceae have become known; these, well illustrated by Pascher's *Rhizochrysis*, are conveniently grouped as Rhizochrysidales. It is evident that rhizopodial members are more plentifully represented in this group than in any other class of the pigmented Protophyta, and an evolution of typical colourless holozoic Rhizopods from members of this phylum is becoming a possibility. Pascher[2] has also described a plasmodial form in which a marked resemblance to Myxomycetes is beyond question. In short the class Chrysophyceae exhibits an astounding diversity of development for which there is perhaps no parallel in the other classes, and it will probably well repay those who take up its study in this country.

Following Senn[3] and Pascher[4] to a large extent, the Chrysophyceae may be grouped as follows:

A. *Chrysomonadales*, including the motile types and their obvious derivatives.

I. *Chromulinales*[5], in which the motile cells bear a single cilium.

II. *Hymenomonadales*[5], in which they bear two equal cilia.

III. *Ochromonadales*, in which there are two unequal cilia.

IV. *Chrysocapsales*, in which the dominant phase is sedentary and palmelloid.

B. *Chrysosphaerales*, the unicellular sedentary "chlorococcoid" type.

C. *Chrysotrichales*, the filamentous forms.

D. *Rhizochrysidales*, the rhizopodial forms.

Of these only the Chrysomonadales and *Phaeothamnion* (Chrysotrichales) are so far recorded in the British Isles; the following key will

[1] Pascher, 1913, p. 89; Pascher, Archiv f. Protistenk. XXXVI, 1915, p. 92, and XXXVIII, 1917, p. 1.

[2] Archiv f. Protistenk. XXXVII, 1916, p. 31 (*Myxochrysis paradoxa*).

[3] Engler-Prantl, Natürl. Pflanzenfam., Teil I, Abt. 1 *a*, 1900, p. 153.

[4] Pascher, 1913, p. 10 et seq.; cf. also Lemmermann, 1910, p. 415.

[5] See what is said on p. 317 as regards the value of this classification based on cilial characters.

serve for the determination of the genera of *Chrysomonadales* concerned:

I. *Chromulinales.*

A. Unicellular, motile, with a simple periplast and simple vacuolar system *Euchromulinaceae*

a. Cells naked *Chromulina*

b. Cells with a rigid envelope[1], distinct from the periplast *Chrysococcus*

B. Unicellular, motile, with a complex periplast and a complex vacuolar system *Mallomonadaceae*

Periplast with imbricating silicified scales, bearing hinged needles *Mallomonas*

II. *Hymenomonadales.*

A. Epiphytic or colonial, with a simple periplast and vacuolar system *Isochrysidaceae*

Cells united to form globular colonies *Syncrypta*

B. Colonial, with a bristly periplast and complex vacuolar system *Euhymenomonadaceae*

a. Colonies spherical, cells ellipsoidal or ovoid *Synura*

b. Colonies band-shaped, cells wedge-shaped *Chlorodesmus*

III. *Ochromonadales.* Only family *Ochromonadaceae*

A. Cells devoid of a special envelope, colonial

a. Cells arranged in spherical or ellipsoidal groups *Uroglena*

b. Cells arranged in a radiating manner in one plane *Cyclonexis*

B. Cells with a special wide envelope, solitary or colonial, epiphytic or free-floating

a. Epiphytic, solitary, envelope with a long, thread-like stalk *Stylopyxis*

b. Rarely epiphytic, solitary, or frequently colonial and then forming dendroid colonies

1. Envelope apparently uniform *Dinobryon*

2. Envelope composed of successive lamellae, whose upper ends project on the outer surface *Hyalobryon*

IV. *Chrysocapsales.*

A. Colonies without definite form, growth not localised *Chrysocapsaceae*

a. Cells grouped within a more or less spherical mass of mucilage *Chrysocapsa*

b. Cells grouped within a cylindrical mass of mucilage, which is sometimes branched *Phaeosphaera*

B. Colonies richly branched, filamentous, with apical growth *Hydruraceae*

Only genus *Hydrurus*

[1] cf. also *Trachelomonas*, p. 414.

GROUP 1. CHRYSOMONADALES

Series I. CHROMULINALES

Family 1. EUCHROMULINACEAE

This comprises the unicellular uniciliate forms with a simple, more or less rigid periplast, and one or two contractile vacuoles. Epiphytic forms with a rigid offstanding envelope are also known, but have not been recorded for the British Isles.

Chromulina Cienkowski, 1870[1]. Unicellular, naked, rarely temporarily colonial, freely motile by means of a single long apical cilium (1–7 times as long as the cell), protoplast usually exhibiting some metaboly. Cells commonly ovoid or ellipsoid, either with a single chromat. having the form of a large curved plate or two laterally disposed chromats., and with a large whitish mass of leucosin at the posterior end; nucleus usually central, one or two contr. vacs. at the front end, eye-spot often recognisable. Multipl. by longit. div. of the motile or resting individuals, in the latter case often with formation of palmelloid stages. Endogenously formed silicified cysts, with a sculptured membrane and a small plugged aperture on one side (cf. p. 315), known in a few sp.

Sp. of this genus are widespread in pure water on the continent, but so far only two are known to occur in this country. *C. ovalis* Klebs (fig. 1, C, p. 22), with cells which are slightly emarginate in front and have a single large chromat., has been observed by the writer in a number of Surrey ponds; cells 6–7 br. and 9–14 l. *C. Rosanoffii* Bütschli (*Chromophyton Rosanoffii* Woron.) (fig. 133, G) occasionally occurs in aquaria and is specially characterised by its method of cyst-formation[2]. The motile individuals come to rest at the water-level and a small knob-like outgrowth, protruded through the surface-film (fig. 133, H), gradually enlarges into a floating spherical cyst containing almost the whole protoplasmic body, only a small stalk-like remnant remaining underneath (fig. 133, I). Since the concave chromatophore reflects the light falling on the cysts, the latter if present in large numbers give a golden-brown sheen to the surface of the water.

Chrysococcus Klebs, 1893[3]. Unicellular and freely motile, the

[1] Cienkowski, Archiv f. mikroskop. Anat. VI, 1870, p. 435; Pascher, Ber. Deutsch. Bot. Ges. XXVIII, 1910, p. 341 et seq.; Pascher, Monogr. u. Abh. Internat. Rev. Hydrobiol. u. Hydrogr. I, 1910, p. 15; Pascher, 1913, p. 13.

[2] Woronin, Bot. Zeit. XXXVIII, 1880, p. 629.

[3] Klebs, Zeitschr. wiss. Zool. LV, 1893, p. 413; Pascher, loc. cit. 1910, p. 28.

naked protoplast enclosed within a spherical or ovoid, smooth or sculptured and often brown-coloured rigid envelope, possessing a narrow apical aperture for the cilium which is 1–7 times the length of the cell. Chromat., etc. as in *Chromulina*. Multipl. by longit. div. of the protoplast, one daughter-individual adopting the envelope of the parent, whilst the other escapes (cf. fig. 133, D) and secretes a new one. Cysts unknown.

Only two sp. have been found in the Brit. Isles and these are rare. *C. rufescens* Klebs (fig. 133, D), with a smooth brown spherical envelope and two lateral chromat., has been recorded from the lake in the Royal Botanic Gardens, Kew (Fritsch, 1906, p. 219); cells 8–11 br. *C. tessellatus* Fritsch (1914, p. 346) was found at Keston, Kent, and is characterised by the tessellate structure of the front half of the envelope and the two small lateral chromats.

Family 2. MALLOMONADACEAE

In this family the uniciliate individuals are provided with a more elaborate periplast and a more complex system of contractile vacuoles. In this country there are only records of the occurrence of species of

Mallomonas Perty, 1852[1]. Unicellular and motile, relatively large, cilium usually not longer than the cell which is of diverse shape and has a periplast in which are deposited numerous small circular or angular silicified imbricating scales, which show regular or irregular arrangement and some or all of which bear delicate hinged (sometimes hollow) siliceous spines, occasionally with fine teeth at the ends. Chromats. two, lateral and parietal; contr. vacs. four or more, lodged at the front or back or in the middle of the cell, whilst in some sp. there is in addition a large anterior non-contractile vac.; nucleus ellipsoidal, often large and distinct. Reprod. by longit. div. and by amoeboid cells escaping from the periplast and giving rise to palmelloid stages. Typical cysts known in several sp.

The sp. of this genus, four of which have been recorded from the Brit. Isles, are typical freshwater plankton-organisms and may at times be dominant. *M. acaroides* Perty, with ovoid or ellipsoid cells (7–12 br.; 20–26 l.), and *M. longiseta* Lemm., with obovoid cells (16–21 br.; 38–46 l.) and transversely arranged scales (fig. 134, D), are both completely covered with backwardly directed spines. In *M. producta* Iwan. (fig. 134, B) the spines are often developed only in the posterior half of the narrow ellipsoidal cell (9–13 br.; 40–70 l.).

[1] Iwanoff, loc. cit. p. 247; Scherffel, loc. cit. 1904, p. 441; Conrad, Archiv f. Protistenkunde, XXXIV, 1914, p. 79; Rehfous, Bull. Soc. Bot. Genève, sér. 2, VII, 1915, p. 128.

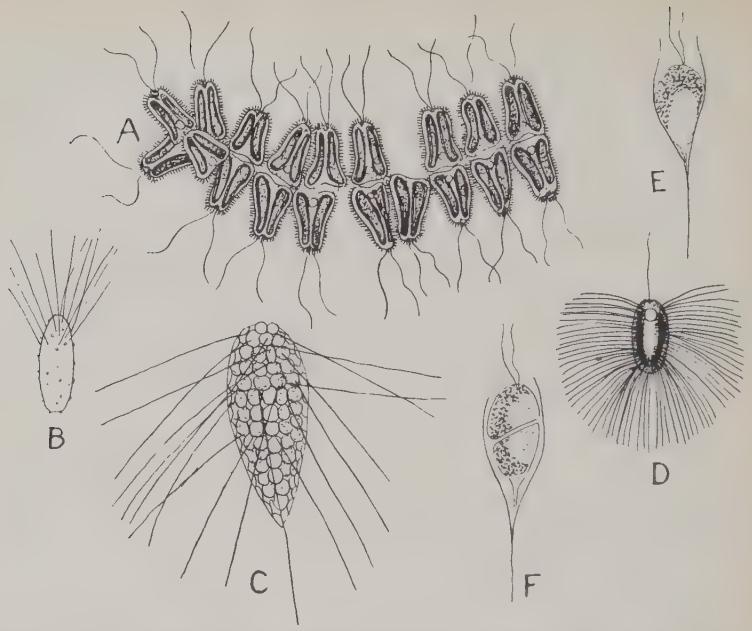

Fig. 134. A, *Chlorodesmus hispidus* Phillips (after Phillips). B, *Mallomonas producta* (Zach.) Iwanoff (after Smith, ×375), anterior end downwards. C, *M. caudata* Iwanoff (after Smith, ×375). D, *M. longiseta* Lemm. (after Lemmermann, ×375). E–F, *Stylopyxis Bachmanni* Fritsch (after Bachmann).

Series II. HYMENOMONADALES

Family 1. ISOCHRYSIDACEAE

Here belong the biciliate forms with a simple periplast and simple vacuolar system. No unicellular motile representatives are known in this family which comprises only colonial and epiphytic types.

Syncrypta Ehrenberg, 1838[1]. Colonies freely motile, globose and compact, composed of closely fitted obovoid cells with a broad anterior end, the whole invested by structureless mucilage, through which the two equal elongate cilia of the individual cells protrude. Chromats. two, lateral; one or two anterior contr. vacs.; protoplast slightly metabolic. Multipl. of cells by longit. div., of colonies by fission. Cysts unknown.

S. Volvox Ehrenb. (fig. 2, C, p. 29), the only sp., is widespread in

[1] Pascher, loc. cit. 1910, p. 36.

standing waters, but usually not abundant. The mucilage-envelope contains minute rods which give it a granulate appearance; cells 7–12 br. and 8–14 l.; colonies 20–70 br.

Family 2. EUHYMENOMONADACEAE

This includes forms with a variously ornamented periplast and a complex anterior vacuolar system. Only colonial representatives are known in this country.

Synura Ehrenberg, 1838[1]. Colonies freely motile, usually destitute of a mucilage-envelope, mostly more or less globose and compact, composed of a variable number (from 2–50) of obovoid or ellipsoid cells which are united by the more or less protracted (sometimes stalk-like) basal ends and have a coarse periplast (or close-fitting envelope?), generally covered with short bristles (but sometimes verrucose or reticulate). Chromats. two, lateral, parietal; several masses of leucosin at back end of cell; nucleus central, spherical, large; no eye-spot; contr. vacs. several, basal and apical, in the latter position often a large non-contractile vesicle; cilia 1–2 times length of cell. Multipl. of cells by longit. div., of colonies by fission; reprod. also by means of naked swarmers which slip out of the periplast and may become amoeboid or form palmelloid stages. Cysts spherical.

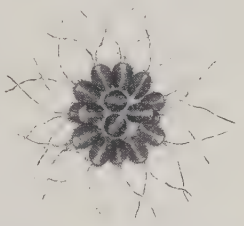

Fig. 135. *Synura Uvella* Ehrenb. Single colony (×400), from Eldwick, W. Yorks.

S. Uvella Ehrenberg (fig. 135), the only Brit. sp., though rare in the plankton of the larger lakes, is commonly found in small ditches and pools, particularly if they are of rain-water, and pure gatherings can frequently be obtained in the early summer; colonies 100–400 br.; cells 8–17 br., 20–40 l. Conrad (1920, p. 176) has recorded colonies with a definite mucilage-envelope, as well as aggregations of 100 and more cells, densely arranged along a gelatinous filament, so as somewhat to resemble *Chlorodesmus*. It is doubtful whether more than one sp. of *Synura* has so far come to light, the diverse ornamentation of the periplast, upon which other sp. have been based, appearing to be a variable feature. According to Moore[2] this genus is responsible for an odour of water resembling that of ripe cucumbers.

[1] Pascher, Archiv f. Protistenk. xxv, 1912, p. 154; Conrad, Bull. Soc. Roy. Bot. de Belgique, xlix, 1912, p. 126; Conrad, Bull. Sci. Acad. Roy. de Belgique, 1920, p. 167; Petersen, Vid. Medd. Dansk. nat. Foren. lxix, 1918, p. 345.

[2] Moore, Yearbook U.S. Depmt. Agric. 1902, p. 184.

Chlorodesmus Phillips, 1882[1]. Colonies freely motile, devoid of a mucilage-investment, band-shaped, composed of a variable number of wedge-shaped cells (oval in side-view), with concave flanks, joined by their broader posterior ends to form a two-ranked aggregate; each cell with a periplast resembling that of *Synura*. Chromats. two, lateral and parietal; no eye-spot; vacuolar system similar to that of *Synura*; cilia as long as the cells. Reprod. unknown.

C. hispidus Phillips (fig. 134, A), the sole sp., has only been recorded from Hertfordshire; it has also been found in the Black Forest, Germany. The cells are 1½–2 times as long as broad, but the actual dimensions are not known. At certain times the colonies exhibit a rhythmic contraction and expansion, the contracted colony being only one-fifth the length of the expanded one.

Series III. OCHROMONADALES

Family OCHROMONADACEAE

The members of this family have two unequal apical cilia and all possess a simple periplast and simple vacuolar system. The unicellular motile genus *Ochromonas* (cf. p. 316) is at present unrecorded for the British Isles, but two colonial types are represented. The family also includes a number of genera in which the individuals are situated within a delicate wide envelope (Lepochromonadineae of Pascher, 1913, p. 60), some of the species being solitary and others colonial. The envelopes are composed of a number of successive thimble-like pieces.

Uroglena Ehrenberg, 1838[2]. Colonies spherical or ellipsoidal, composed of ovoid or ellipsoidal cells, situated at slight intervals at the periphery of a mass of mucilage and tapering at their inner ends into thread-like (hollow?) mucilage-strands forming a forking system meeting in a common centre (fig. 136, A). Chromat. a curved parietal plate, with a rod-shaped eye-spot at the front end; two anterior contr. vacs.; nucleus central. Multipl. of cells by longit. div., of colonies by bipartition. Cysts spherical, with a membrane bearing prominent pointed spines and a long tubular process on one side (fig. 136, C).

U. Volvox Ehrenb. (fig. 136, A–C) is found in the same situations as *Syncrypta* and *Synura*, but is far less abundant. The colonies are 40–400 br. and the cells 12–20 l. and 8–13 br.; the longer cilium is 2–3 times as long, the shorter about as long as the cell.

[1] Phillips, Trans. Herts. Nat. Hist. Soc. II, 1882, p. 92.

[2] Zacharias, Forschungsber. Plön, III, 1895, p. 78; Petersen, loc. cit. p. 353; Iwanoff, loc. cit. p. 254.

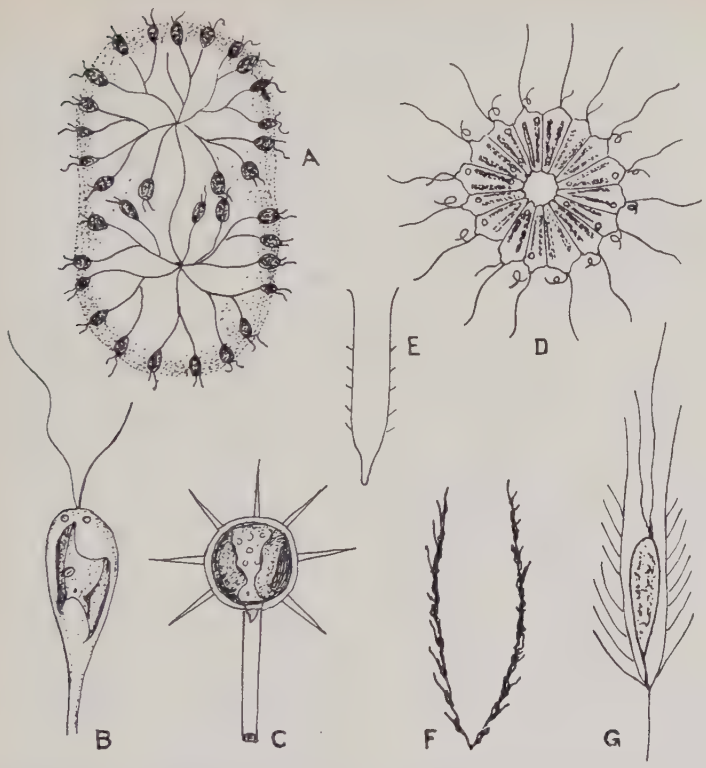

Fig. 136. A–C, *Uroglena Volvox* Ehrenb.; A, colony about to divide (after Zacharias); B, single individual, and C cyst (after Iwanoff, ×1000). D, *Cyclonexis annularis* Stokes (after Stokes, ×750). E, *Hyalobryon mucicola* (Lemm.) Pascher (after Smith, ×1000). F, *Dinobryon utriculus* Stein, disorganising envelope (after Pascher). G, *Hyalobryon mucicola* (Lemm.) Pascher (after Bachmann, ×700).

Cyclonexis Stokes, 1886[1]. Colonies composed of 10–20 narrow wedge-shaped cells with a pointed anterior end, arranged in one plane and closely connected to form a circular group surrounding a small central space; young colonies somewhat funnel-shaped. Chromats. two, lateral; no eye-spot; two anterior contr. vacs. Reprod. and cysts unknown.

C. annularis Stokes (fig. 136, D) is a very rare form, recorded by G. S. West from Lapworth, Warwickshire (Grove, 1920, p. 2); cells 11–14 l.; one cilium as long, the other half as long as the cell.

[1] Stokes, Proc. Amer. Phil. Soc. XXIII, 1886, p. 564, and Journ. Trenton Nat. Hist. Soc. 1888, p. 117.

Stylopyxis Balachonzeff, 1909[1]. Epiphytic, non-colonial, cells obovoid, seated at the base of a delicate stalked envelope with a wide aperture, the stalk as long as the envelope. Chromats. two, lateral; contr. vacs. two, apical. Reprod. by transv. div., the one daughter-individual escaping as an *Ochromonas*-like swarmer. Cysts unknown.

Bachmann (1907, p. 82) has recorded a form found epiphytic on *Coelosphaerium Naegelianum* in Loch Lochy, Scotland, under the name *Stylochrysalis aurea* (Chod.) Bachm., regarding it as synonymous with *Stylococcus aurea* Chod.; the identity of the two organisms is however very questionable. Bachmann's form, as figured by him, displays far more resemblance to the genus *Stylopyxis* than to *Stylochrysalis*, except in the cilial characters; his fig. 20 (loc. cit. p. 80), however, shows some inequality in the cilia, and the writer is of opinion that it would best be regarded as a sp. of the former genus (*S. Bachmanni* Fritsch[2] (fig. 134, E, F)).

Dinobryon Ehrenberg, 1833[3]. Solitary or forming dendroid colonies, the solitary forms in part epiphytic, the others freely motile; cells enclosed in a wide campanulate or cylindrical, smooth or undulate cellulose envelope, which is attenuated at the base into a straight or obliquely disposed point, has an aperture transverse or oblique to the longit. axis, and is hyaline or sometimes coloured yellow or brown by oxide of iron. Cells delicate, elongate, oval or pyriform, metabolic, drawn out at the lower end into a short contractile stalk which is attached a little to one side of the base of the envelope, while the hyaline apex of the protoplast is hollowed out to form a kind of mouth through which solid particles can be ingested; chromats. one or two, parietal, yellow-brown; eye-spot usually distinct; contr. vacs. in various positions, usually central or basal; large glistening lumps of leucosin frequent at the posterior end. Multipl. by longit. div., one daughter-individual in the solitary types escaping as an *Ochromonas*-like swarmer and subsequently forming a new envelope; in the colonial types one or both daughter-individuals effect a lodgement at the inner edge of the rim of the parent-envelope and there secrete a similar envelope whose mode of formation is described on p. 319. The cells may also occasionally escape as swarmers without previous division. Cysts frequent, spherical, silicified, with a short projecting

[1] Pascher, 1913, p. 62.

[2] cf. also Pascher, 1913, p. 63.

[3] Klebs, loc. cit. 1892, p. 413; Lemmermann, Ber. Deutsch. Bot. Ges. XVIII, 1900, p. 500; Brunnthaler, Verh. Zool.-Bot. Ges. Wien, LI, 1901, p. 293; Lemmermann, 1910, p. 452; Pascher, 1913, p. 63; Petersen, loc. cit. p. 353.

process (fig. 137, B, C), either lodged within the envelope or within a special spherical membrane connected with, and just outside, the aperture of the envelope.

Apart from *D. calyciforme* Bachmann (1907, p. 82), which is a little known epiphyte found once on the mucilage-envelope of *Coelosphaerium Naegelianum* in Loch Earn, Scotland, and the free-floating *D. crenulatum* W. & G. S. West (1909, p. 325), only colonial types have so far been recorded in this country. They are very abundant in the freshwater plankton, but specific determination is usually a matter of considerable difficulty as there are manifold transitions

Fig. 137. A, *Dinobryon cylindricum* Imhof var. *divergens* (Imhof) Lemm.; two individuals from Eldwick, W. Yorks (×730). B, encysted condition of same. C, *D. Sertularia* Ehrenb., colony with individuals encysted, from Cornwall (×410). *c*, cysts.

between the different forms and no two authorities are agreed on their classification. In several of the species involved it is known moreover that the colonies are shorter and more compact and the envelopes less elongate in spring than in summer. The few remarks that can be made here about the more frequent of the six or seven Brit. sp. are inadequate to characterise them, and no one should attempt determination of these forms without reference to one of the standard works. The most widely distributed sp. is *D. divergens* Imhof (fig. 137, A, B), which by many is regarded as a variety of the less abundant *D. cylindricum* Imhof; in the former the colonies are spreading and loosely branched and the base of the envelope is obliquely

pointed. Another frequent sp. is *D. Sertularia* Ehrenb. (fig. 137, C), with compact densely branched colonies and a usually symmetrical vase-shaped envelope; the closely allied *D. protuberans* Lemm., with a more cylindrical envelope, is likewise not uncommon. *D. sociale* Ehrenb., with narrow elongate colonies of densely placed individuals having cone-shaped envelopes, is not so widely distributed.

Hyalobryon Lauterborn, 1896[1]. Solitary or more rarely colonial, primarily always epiphytic; cells enclosed in a wide delicate envelope as in *Dinobryon*, but the edges of the successive thimble-like strata of which the latter is composed project either throughout the whole length (fig. 136, E, G) or only in the upper part of the envelope; in all other respects there is close resemblance to *Dinobryon*. Chromats. two, of unequal size; contr. vacs. apical or central. Multipl. by transv. (?) div.; in the colonial sp. the daughter-individuals are attached to the outer side of the envelope of the parent. Cysts similar to those of *Dinobryon*.

The sp. of this genus are specially met with in pools of pure water and ponds containing abundant aquatics, but are easily overlooked owing to the delicate texture of the envelope. All are epiphytes, often attached to larger plankton-organisms. The only record for the Brit. Isles is *H. mucicola* Pascher (*H. Lauterbornii* Lemm. var. *mucicola* Lemm. (fig. 136, E, G)) found on *Coelosphaerium Naegelianum* in Loch Earn; the envelope is 25–50 l.

Series IV. CHRYSOCAPSALES

Family 1. CHRYSOCAPSACEAE

This includes a few palmelloid types in which the cells are embedded in mucilage without any definite arrangement. Reproduction is effected by periodic swarming of the individuals.

Chrysocapsa Pascher, 1913[2]. Colonies free-floating, more or less spherical or ellipsoidal, containing loosely spaced spherical or ellipsoid cells in groups of two, four, eight, etc. within often relatively firm mucilage. Chromats. one or two, parietal, frequently with a red pigment-spot. Multipl. of cells by longit. div. or by div. in all directions (?). Swarmers ovoid or subpyriform, with a single cilium or with two equal cilia. Cysts not observed.

[1] Lauterborn, Zool. Anzeiger, XIX, 1896, p. 17; Zeitschr. wiss. Zool. LXV, 1899, p. 377; Lemmermann, Forschungsber. Plön, X, 1903, p. 166; Pascher, loc. cit. 1910, p. 58.

[2] Pascher, 1913, p. 85; cf. also Archiv f. Protistenk. LII, 1925, p. 548.

Neither of the two Brit. sp. is properly known and they are possibly not closely allied. *C. paludosa* (W. & G. S. West) Pascher (*Phaeococcus*[1] *paludosus* W. & G. S. West, 1903, p. 34) (fig. 138) is a rare form in moorland pools; cells 6–11 br.; colonies up to 100 br. *C. planctonica* (W. & G. S. West) (*Phaeococcus planctonicus* W. & G. S. West[2], 1905, p. 496) has been found in the Scotch and Irish plankton; cells globose, 7·2–9·6 br.

Fig. 138. *Chrysocapsa paludosa* (W. & G. S. West) Pascher, from Eldwick, W. Yorks (×410). *z*, zoospores.

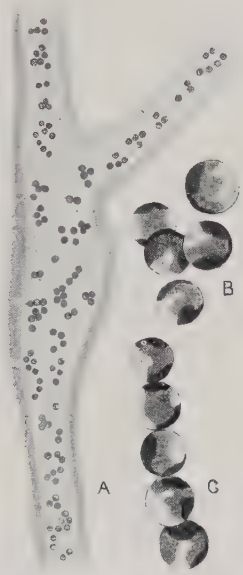

Fig. 139. *Phaeosphaera gelatinosa* W. & G. S. West. A, portion of colony (×50). B and C, cells showing the single chromatophore (×410). From Tremethick Moor, Cornwall.

Phaeosphaera W. & G. S. West, 1903[3]. Colonies of large, exactly spherical cells with a thin membrane, embedded in small groups in an extensive gelatinous cylinder which is sparsely branched. Chromat. one, parietal, with somewhat irregular margins. Cell-div. in three directions. Reprod. unknown.

[1] *Phaeococcus* is a genus of Cryptophyceae not yet found in this country (cf. p. 389).

[2] Pascher (loc. cit. 1925, p. 545) places this species, which is wrongly ascribed to G. M. Smith, in a separate genus of Chrysosphaerales, but this hardly seems warranted in the present state of our knowledge. *Chrysocapsa planktonica* Pascher (1913, p. 86), which is not the same as West's species, should be renamed *C. Pascheri*.

[3] West and West, 1903, p. 34.

P. gelatinosa W. & G. S. West (fig. 139) is known only from *Sphagnum*-bogs in Cornwall: cells 14–17·5 br.: investment 80–200 br.

Family 2. HYDRURACEAE

This includes only the unique genus

Hydrurus Agardh. 1824[1]. Colonies appearing as richly branched feathery brown tufts (fig. 140, A), attached to stones and rocks in mountain streams and composed of tough, almost cartilaginous, cylindrical mucilage-strands in which are embedded numerous naked cells, at first spherical and later ellipsoidal or pear-shaped. Cells in each strand show a dense peripheral and looser central aggregation (fig. 133, A); a single curved chromat. containing a pyrenoid-like body occupies the anterior, often pointed and upwardly directed end, whilst the broadened, downwardly directed posterior end of the cell harbours the contr. vacs. (5–6) and leucosin. Each branch grows apically, the terminal cell undergoing repeated longit. div., one half reconstituting the "apical cell," the other contributing to the lengthening of the branch: new branches arise mainly in acropetal succession. The mucilage seems to be secreted largely by the posterior end of the cell. Reprod. by swarmers whose formation is confined to the short branches and ensues after longit. div. of series of cells: swarmers 1-ciliate, tetrahedral, the front end drawn out into three slightly amoeboid processes, the back end pointed and harbouring the chromat. (fig. 140, B). The swarmers become attached by their front end and immediately secrete a mucilage-cylinder in which longit. div. of the protoplast commences: certain of the peripheral cells take on the functions of apical cells and produce branches. Cyst-formation during the summer months in certain cells which are carried out in mucilage-strands beyond the general surface (fig. 133, B): within each cell a silicified membrane, with the customary pore and plug, is secreted: mature cysts biconvex, with a broad delicate wing extending round half the periphery. *Palmella*-stages also observed, but imperfectly known.

Fig. 140. *Hydrurus foetidus* (Vill.) Kirchn. A, nat. size. B, swarmer (after Lagerheim).

This genus is highly specialised. In its marked individuality and division of labour it ranks as high as, if not higher than, such

[1] Berthold, 1878, p. 176; Lagerheim, Ber. Deutsch. Bot. Ges. vi, 1888, p. 73.

a form as *Draparnaldia* (p. 186). In the absence of a cell-wall and of sexual reproduction, however, it betrays a lower level in the phylogenetic series.

H. foetidus (Vill.) Kirchn. (fig. 140) is common in the alpine streams of Central Europe and in the Arctic regions, when the snows melt in spring, but in the Brit. Isles it is of very rare occurrence, being known only from Scotland, Yorkshire, and Devonshire. The plants are 1–30 cm. long, of an olive-green colour and sticky, and give off an offensive odour when alive. The colony is simple below, but branched above, often cut up into fine penicillate divisions and covered with small villous projections giving it a plumose appearance. Occasionally it is densely encrusted with carbonate of lime.

GROUP 3. CHRYSOTRICHALES

Family PHAEOTHAMNIONACEAE

The only British representative is the rare genus *Phaeothamnion* Lagerheim, 1884[1]. Short, branched or unbranched filaments, epiphytic on larger Algae by means of a

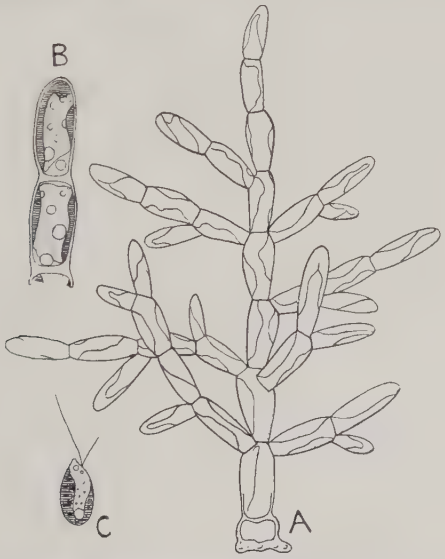

Fig. 141. *Phaeothamnion confervicolum* Lagerh. (after Pascher). A, habit; B, two cells from the end of a branch; C, swarmer. B and C are regarded by Pascher as belonging to a distinct species.

[1] Lagerheim, Bih. K. Sv. Vet.-Akad. Handl. IX, 1884, No. 19; Borzi, Atti Congr. Bot. Internaz. Genova, 1892, p. 454; Pascher, loc. cit. 1925, p. 498.

more or less hemispherical practically colourless basal cell with a thick membrane; cells cylindrical with cellulose walls, which readily become mucilaginous, and a lobed parietal chromat. (several discoid chromats. in a recently described species). Reprod. by liberation of one or two (rarely 4–8) swarmers, with two unequal cilia and an eye-spot, through a lateral aperture in the wall; these swarmers may (*a*) germinate directly to form new plants or (*b*) give rise by rounding off and repeated div., accompanied by mucilage-formation, to *Palmella*-stages. The latter may also originate from the ordinary plants. The cells of the *Palmella*-stages either produce swarmers or give rise to spherical silicified cysts like those of other Chrysophyceae; in germination the cysts form one or two swarmers. The sex. reprod. described by Borzi is probably a misinterpretation.

This genus has been regarded as a member of the Cryptophyceae, but Pascher has recently shown conclusively that it belongs to the Chrysophyceae.

P. confervicolum Lagerh. (fig. 141), the only Brit. sp., has been recorded by M'Keever[1] from Upper Elf Loch, Midlothian; cells 3–9 br.

[1] M'Keever, Trans. and Proc. Bot. Soc. Edinburgh, xxiv, 1912, p. 176.

CLASS IV. BACILLARIALES (DIATOMALES)

The Diatoms are unicellular, sometimes colonial, plants which enjoy a very wide distribution in all kinds of habitats and play a very important rôle, especially in the aquatic vegetation of the world. They appear as a sharply circumscribed class of rather highly evolved forms which afford few points of vantage either for the tracing of their phylogeny or of their affinities with other groups of Protophyta. Pascher[1] has collected together evidence indicating a relationship with Heterokontae and Chrysophyceae (cf. p. 350), and this certainly seems more clearly founded than the older views relating the Diatoms to Phaeophyceae or Conjugatae, the resemblances in both these cases appearing purely superficial.

The remarkable sculpturing of the silicified cell-walls renders Diatoms objects of great beauty and, as a consequence, they have long been made the subject of special study by microscopists. The walls are composed of a matrix of pectin impregnated with silica, but the outer, often mucilaginous, portion consists of pectin only and can frequently be readily demonstrated by slight staining with aniline dyes[2]. The silica can be removed by the action of hydrofluoric acid, leaving the pectin behind; or the latter can be removed by calcination or maceration, leaving only the siliceous constituent[3]. Specific determination, in the vast majority of cases, is based on the characteristic markings, etc. of the silicified membranes.

The Diatom-cell (often spoken of as a *frustule*) has a wall composed of two distinct and usually equal halves, the older (*epitheca*) fitting closely over the younger (*hypotheca*) (fig. 142, B, C). Each half consists of (*a*) a thin, commonly somewhat convex *valve* the edges of which are slightly incurved and attached to (*b*) a *connecting-band* (fig. 142, C, *cb*, *cb'*) in the form of a closed or open hoop with overlapping edges[4]; it is the two connecting-bands, together forming the *girdle*, that fit over one another. Thus, the individuals of the very common Diatom-genus *Navicula* (fig. 142, A, B) have the general form of the oblong boxes in which preserved dates are usually sold, whilst in such a form as *Cyclotella* (fig. 147, B, C) the frustule may be

[1] Pascher, 1914, p. 145; Pascher, 1921.

[2] Mangin, Compt. Rend. CXLVI, 1908, p. 770, and Ann. Sci. Nat., Bot., sér. 9, VIII, 1908, p. 177.

[3] cf. p. 16.

[4] Palmer and Keeley, Proc. Acad. Nat. Sci. Philadelphia, 1900, p. 465.

likened to a circular pill-box; in either case the bottom and top of the box correspond to the two valves, the sides to the two overlapping connecting-bands. It will be apparent therefore that the Diatom-cell may be regarded from two aspects, that in which one or other valve is seen (*valve-view* (fig. 142, A; 147, B)) and that in which the girdle is exposed to view (*girdle-view* (fig. 142, B; 147, C)); whilst the latter is very commonly rectangular in outline, the valve-view varies very much in shape in the different genera and species.

In a large number of freshwater Diatoms the valves are elongated and, with reference to their median (so-called *sagittal*) axis either show isobilateral (e.g. *Navicula* (fig. 142, A); *Synedra* (fig. 152, A)) or zygomorphic (e.g. *Gomphonema* (fig. 160, A)) symmetry, or are altogether asymmetric (dorsiventral, e.g. *Cymbella* (fig. 143, E; 162, A)). All such elongate Diatoms are classed as Pennatae, in contrast to the Centricae which have radially symmetrical valves (e.g. *Cyclotella* (fig. 147, B)). The centric Diatoms are far more abundant in the sea than in freshwater, and the marine forms, moreover, attain a much larger size than the freshwater ones. In recent years doubts have been expressed as to whether centric and pennate Diatoms are as closely related as is generally assumed, a matter which will be referred to again below.

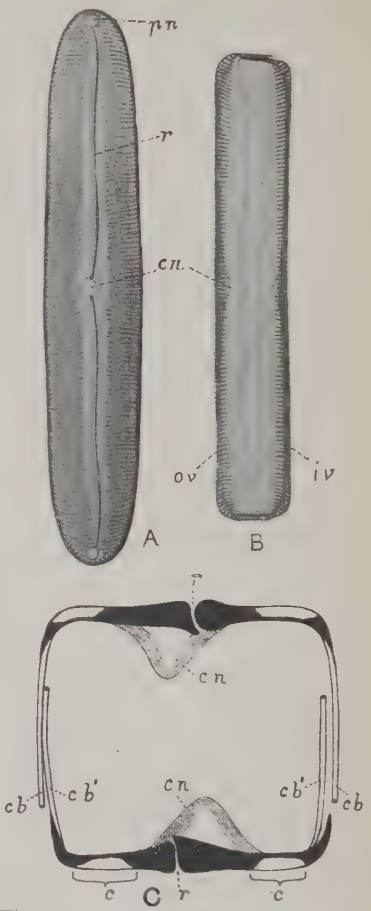

Fig. 142. A, valve-view of *Navicula nobilis* Ehrenb. var. *Dactylus* (Ehrenb.) Van Heurck, from Dolgelly, Wales (×250). B, girdle-view of *N. major* Kütz., from Shipley, W. Yorks (×300). C, Transverse section of frustule of *Navicula* (from Van Heurck, after W. Prinz, very highly magnified). *c*, costa; *cb* and *cb'*, the two connecting-bands forming the girdle; *cn*, central nodule; *iv*, inner valve; *ov*, outer valve; *pn*, polar nodule; *r*, raphe.

Since the valve is usually the most characteristic part of the

Diatom-frustule, a brief consideration of some of its more outstanding features will help towards an initial comprehension of the group. In nearly all cases the valves are ornamented with striae which in the centric Diatoms are radially disposed (fig. 147, D) and in the pennate types are arranged in two series, one on either side of the valve (figs. 142, A; 156). In forms like *Synedra* (fig. 152, A) and *Fragilaria* (fig. 152, C) the two systems of striae are separated by a narrow linear smooth area (*axial area*) occupying the sagittal axis. This smooth area is often spoken of as a *pseudo-raphe*, since it simulates the true raphe found in

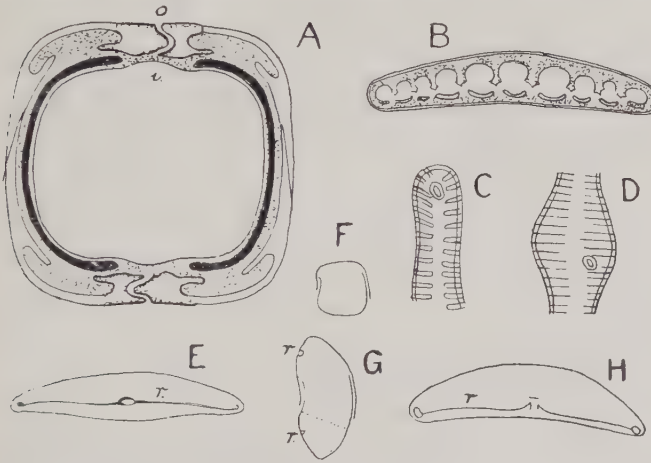

Fig. 143. A, *Navicula* (*Pinnularia*) *viridis* Kütz., transverse section of frustule (after Lauterborn); the inner (*i*) and outer (*o*) fissures of the raphe are shown, the protoplasm is dotted, and the two chromatophores shown dark. B, *Epithemia Argus* Kütz. var. *alpestris* Rabenh., septum from one of the intercalary bands (after Müller). C, *Synedra splendens* Kütz., apex of valve with pore (×1650, after Müller). D, *Tabellaria fenestrata* (Lyngb.) Kütz., central part of valve with pore (×1650, after Müller). E, valve, and F, section of frustule of *Cymbella* (after Müller). G, section of frustule, and H, valve of *Amphora ovalis* Kütz. (after Müller). *r*, raphe.

this position in *Navicula* (fig. 142, A, *r*), *Gomphonema* (fig. 160, A), etc. In these genera the smooth axial area is usually wider and shows a *central* (fig. 142, A, *cn*) and two *polar* (*pn*) *nodules* which are internal thickenings of the wall (cf. fig. 142, C); between the central and each polar nodule there extends a well-marked line, actually a slit in the valve, and this constitutes the true *raphe* which will be dealt with more fully below. In *Stauroneis* (fig. 156, E) the central nodule extends as a *stauros*[1] over the whole width of the valve, whilst in *Amphipleura* (fig. 157, C) it is greatly elongated. In *Achnanthes* and *Cocconeis*

[1] The striations are not developed over the region of the stauros.

one valve possesses only a pseudo-raphe (fig. 155, B and D), the other a true raphe with both central and polar nodules (fig. 155, A and E).

In all the genera just mentioned the valves are symmetrical about the median line, but in a number of others they are dorsiventral. Thus in *Cymbella* (figs. 143, E; 162, A) and *Amphora* (figs. 143, H; 162, B) the valves, as well as the raphe, are more or less curved and the raphe tends to lie nearer to the ventral (plane or concave) than the dorsal (convex) side. In both genera too the connecting-bands are more strongly developed on the dorsal than on the ventral surface, so that the valves are slightly tilted and one girdle-view is broader than the other (fig. 143, F). In *Amphora*, moreover, the valves are no longer plane, but shaped like a gable in transverse section (i.e. crested (fig. 143, G)), and these features are responsible for the fact that individuals of this genus nearly always present their girdle-view to the observer (fig. 162, C). In *Rhopalodia* much the same thing obtains, but the raphe is lodged in the crest of the gable (fig. 161, G) and not along one of its sloping sides as in *Amphora*, so that in the girdle-view the raphe is seen immediately adjacent to the dorsal edge of the valve[1].

Dorsiventral types are encountered also among the Diatoms provided only with a pseudo-raphe, and in this case the latter may be situated in the middle of the valve (*Ceratoneis* (fig. 154, D)) or along the ventral surface (*Eunotia* (fig. 154, A, B)). In *Ceratoneis* central and polar nodules are present, but in *Eunotia* only the latter are found and are usually obvious both in the valve- and the rectangular girdle-views (fig. 154, C).

A somewhat different type of valve-structure is seen in the Nitzschioideae[2]. Here the valves are possessed of a slightly projecting keel which runs along their whole length, is marked with evenly spaced (circular or rod-shaped) carinal dots (cf. fig. 164), and contains a true raphe in the form of a longitudinal canal without central or polar nodules. In *Bacillaria* (fig. 164, I) the keel is median, whilst in *Nitzschia* (fig. 164, A, B, F–H) and *Hantzschia* (fig. 164, E) it is displaced towards one side of the valve. In *Nitzschia* the keels of the two valves are placed diagonally so that the two sets of carinal dots do not lie on the same girdle-face, whilst in *Hantzschia* the keels occupy adjacent angles and both appear on the same girdle-face; in these two genera, moreover, the section of the frustule is not square as in *Navicula*, but rhombic (fig. 164, D).

[1] cf. especially Müller, Ber. Deutsch. Bot. Ges. XIII, 1895, p. 222 et seq., and Engler Bot. Jahrb. XXII, 1895, p. 54.

[2] Pfitzer, Hanstein's Bot. Abhandl., Heft 2, 1871, p. 95.

In the complex genus *Surirella*, lastly, the valve-view, which is commonly elliptic or oval (fig. 166, A), shows a prominent median pseudo-raphe with a system of strong ribs on either side. The two margins of each valve are winged (fig. 144, C), and the entire length of the somewhat dilated outer edge of each wing is occupied by a narrow slit-like canal (raphe) communicating with the external medium; each valve therefore possesses two raphes, but there are no nodules. The wings, as is usually plainly seen in the (often rhombic) girdle-view, contain a system of rather narrow transverse canals through which the protoplasm of the cell communicates with that in the raphe, these canals being separated from one another by broad intervening strips of membrane (fig. 144, D). The brief account that has just been given by no means exhausts the diversity of outward form, as the subsequent consideration of the genera will show.

The simple structure of the frustule described at the outset is complicated in many Diatoms by the interposition of *intercalary bands*[1] between the valves and their connecting-bands, which in such cases are the last parts of the wall to be formed. These intercalary bands are usually well seen in the girdle-view, e.g. in *Tabellaria* (fig. 149, F). The figure also shows short (longitudinal) *septa* arising from these intercalary bands (2–12 in number) parallel to the valves and extending from the poles into the interior of the cell, so as to divide it up into a number of compartments; the septa do not however reach to the centre of the frustule (cf. also fig. 149, E, G) and successive septa arise from alternate ends of the latter. In some species of *Epithemia* the single intercalary band in each half of the frustule bears a longitudinal septum, extending right across the latter parallel to the valves and perforated by a series of rounded apertures (fig. 143, B) which lead into chambers between the septum and the valve; these chambers are cut off from one another by a system of further (transverse) septa placed at right angles to the valve, which appear as prominent ribs in the valve-view (fig. 163, B) and are also seen in the girdle-view (fig. 163, C). Similar transverse septa are developed in *Denticula* (fig. 150, C, D). The elongate-cylindrical frustules of *Rhizosolenia* (fig. 148, A, D) have asymmetrical valves each furnished with a long seta, while the long intervening girdle is composed of numerous scale-like intercalary bands which are more or less imbricate. In all cases the connection between the valves and the connecting-bands, as well as between them and the intercalary bands when present, is a firm one and there are often flanges which serve to strengthen the junction.

[1] O. Müller, Ber. Deutsch. Bot. Ges. IV, 1886, p. 306.

The *striae*, which are such a customary feature[1] of the valves of Diatoms, are, with the best lenses, in the majority of forms found to consist of linear series of small dots (*punctae* (cf. fig. 161, C, D)) due to cavities (areolae) situated within more or less pronounced ridges of the wall which project either towards the inside or the outside. It is the close and regular arrangement of the punctae that causes them to appear as striae. They are so extremely fine and constant in arrangement in some species (e.g. *Amphipleura pellucida*) as to furnish splendid test-objects for the definition and angular aperture of microscope-lenses. All gradations exist from very fine striae to conspicuous ribs or *costae* (fig. 162, A), but these latter are not always composed of series of punctae. In the large *Naviculas* of the section *Pinnularia* they represent transversely distended chambers within the inner part of the wall (cf. fig. 143, A), communicating with the cell-cavity by oval foramina, whose edges appear as a pair of fine longitudinal lines running over the system of transverse costae[2] (cf. fig. 144, A). In the centric Diatoms some of the larger cavities (areolations) may be widely open, either to the exterior or the interior, but this is probably not the case in the majority of pennate forms. A notable exception, apart from the *Pinnularias* just mentioned, is formed by the species of *Epithemia* where rows of circular cavities, appearing as punctae and open towards the interior of the cell, occur between the ribs on the valves. The thin portions of the wall that separate the cavities from the interior or exterior, as the case may be, are in many Diatoms traversed by very fine canals (pores), which are only to be detected under the highest magnifications; such pores are altogether lacking however in *Pinnularia*. Large obvious pores are often found at points where local secretion of mucilage occurs (cf. p. 344). Müller recommends treatment with hot sodium carbonate and potash in studying the structure of the valves[3].

The cytoplasm[4] usually forms a thin lining layer which often extends into all the cavities within the wall (figs. 143, A; 144, C). The vacuole is bridged by a conspicuous transverse strand occupied by the rounded or oval nucleus (figs. 144, C; 157, E, F). A very weak solution of methylene blue will bring out the nucleus in living Diatoms, staining it clearly before the rest of

[1] In a few species of *Navicula* (e.g. *N. perlepida* Grun.) the very thin wall is apparently structureless.

[2] Transverse costae of another kind are seen on the valves of many forms provided with transverse septa (e.g. *Denticula*, *Diatoma*, *Meridion*, etc.).

[3] cf. especially Müller, Ber. Deutsch. Bot. Ges. XVI, 1898, p. 386; XVII, 1899, p. 423; XVIII, 1900, p. 480; XIX, 1901, p. 195.

[4] cf. Lauterborn, Unters. üb. Bau, Kernteilung, u. Bewegung d. Diatomeen, Leipzig, 1896, p. 17; Pfitzer, loc. cit.

the protoplasm. In *Surirella* a slight hollow on one side of the nucleus is occupied by a centrosome which is recognisable in the living cell; a similar body has been found in some *Pinnularias*.

One (e.g. *Cymbella*, *Surirella*) or many chromatophores[1] may be present in the cells; they may be small and discoid (especially in centric types (fig. 146, E)), large and plate-like (fig. 157, D, E), band-shaped, or extensive lobed structures occupying a large part of the lining cytoplasm (e.g. *Cymbella*). The extremely irregular chromatophores of some species are perforated at various points. Where septa are present within the frustules, lobes of the chromatophores usually extend into the chambers produced by them. The chromatophores are yellow- or golden-brown in colour, or very rarely green[2] (e.g. some forms of *Navicula viridis* and *N. cuspidata*). They contain the usual pigments, but these are masked by the presence of a brown pigment, *diatomin*, soluble in water and very similar to, or perhaps identical with, the fucoxanthin of the Phaeophyceae; this accessory pigment still awaits a full investigation[3].

The chromatophores of Diatoms generally contain naked pyrenoids (absent in most *Naviculas*, but not in *Pinnularia*), which often project from the internal face of the plastid as rounded elevations and are variable both in number and arrangement. Mereschkowsky[4] records pyrenoids which had partially or entirely separated from the chromatophores, appearing as free colourless bodies on their inner surface. It may be doubted whether the pyrenoids of Diatoms are directly comparable with those of Isokontae.

The products of photosynthesis would appear in the main to accumulate as drops of fatty oil which are usually conspicuous in the cells under favourable conditions of nutrition. Side by side with them other globules occur which have been identified as volutin by A. Meyer[5]. They are faintly bluish and doubly refractive, do not stain with osmic acid, and are insoluble in alcohol and ether; in living cells treated with methylene blue they take on a deep reddish-violet tint. The nucleus is often surrounded by small rods grouped in pairs, the nature and function of which are unknown.

[1] cf. especially Mereschkowsky, Script. Bot. Hort., Petropol. XXI, 1903, p. 107; Heinzerling, Bibl. Bot., Heft 69, 1908, p. 10.

[2] Some species of *Nitzschia* (e.g. *N. putrida* Benecke, Jahrb. Wiss. Bot. XXXV, 1900, p. 535; Richter, Denkschr. Akad. Wien, Mat.-nat. Kl. LXXXIV, 1909, p. 657) are colourless saprophytes. Karsten (Flora, LXXXIX, 1901, p. 414) found that *N. palea*, when cultivated in glycerine or grape sugar, lived as a saprophyte and exhibited extreme reduction of the chromatophores.

[3] cf. however Molisch, Mikrochemie, 1923, p. 257.

[4] Flora, XCII, 1903, p. 77.

[5] Bot. Zeit. LXII, 1904, p. 139.

Many free unattached members of the Pennatae exhibit spontaneous movements the mechanism of which, in spite of much research, cannot yet be said to be fully clear. This power of locomotion is specially marked in the naviculoid forms, some of which execute very slow movements (e.g. *Amphipleura*),

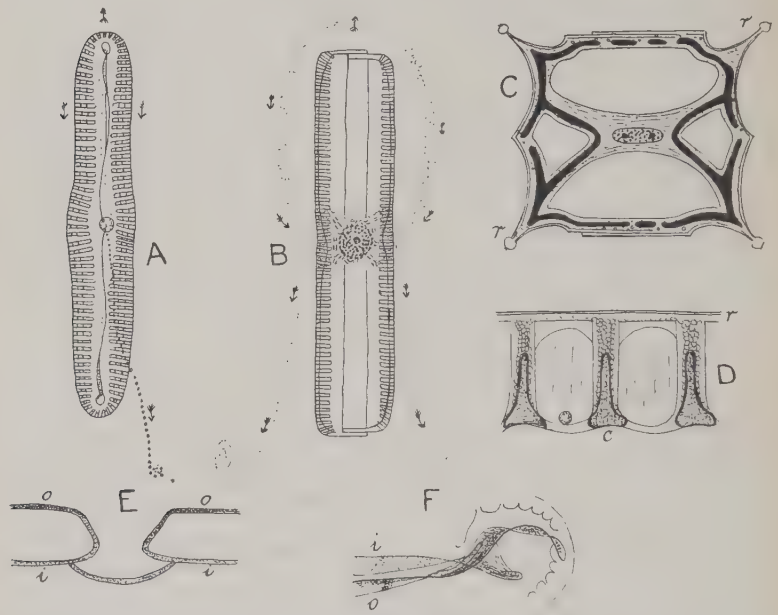

Fig. 144. A–B, *Navicula* (*Pinnularia*) *viridis* Kütz.; A, valve-, and B, girdle-view; the dots indicate threads of mucilage with adhering sepia particles, the arrows showing the direction of movement of the latter (after Lauterborn, from Oltmanns). C–D, *Surirella Capronii* Bréb. var. *calcarata* (Pfitzer) Hustedt; C, transverse section of frustule, and D, longitudinal section of one of the four wings; *r*, raphe-canal; *c*, transverse canal communicating with raphe and occupied by protoplasm continuous with that in the frustule (after Lauterborn, from Oltmanns). E–F, *Navicula viridis* (after Müller); E, longitudinal section of central nodule, showing the canals joining the outer (*o*) and inner (*i*) fissures, and the connection between the latter; F, terminal nodule showing the ends of the two fissures.

whilst others progress with considerable rapidity backwards and forwards in the direction of their longitudinal axis. The motion is occasionally creeping and steady, more frequently jerky, and sometimes, but not necessarily, takes place along some kind of substratum with which the Diatom is in contact. Some *Naviculas* perform pendulum-like movements about one

fixed end (cf. *Closterium*). The individuals of *Surirella* exhibit a peculiar rolling and turning motion.

It is a significant fact that movement occurs only in those forms which possess a true raphe, i.e. a slit-like canal extending through the length of the valve[1]. In *Surirella*, *Rhopalodia*, and the Nitzschioideae the raphe is a simple canal as described above (p. 338); it contains protoplasm which is connected with that in the interior of the cell and also with the external medium[2]. In the Naviculoideae, however, the raphe, which in the valve-view appears as two separate slightly curved lines (figs. 142, A; 144, A), is far more complex[3]. In *Navicula* itself a transverse section of the valve (fig. 143, A) shows the raphe as a V-shaped cleft, open both towards the outside and inside, but often closed at the apex of the V; there are thus really two separate superposed fissures (outer and inner) extending from the central nodule to each polar nodule. At the central nodule (fig. 144, E) the two overlying fissures (*o* and *i*) approaching from each end are connected by a loop, whilst the inner fissures are placed in communication by a fine horizontal canal extending through the inner part of the central nodule. Within the hollow polar nodules the outer fissures terminate as curved slits (*terminal fissures* (fig. 144, A and F)) which usually, though not always, curve in the same direction at the two ends of a valve, but are invariably curved in opposite directions in the two valves of a frustule. The inner fissure (fig. 144, F) enlarges into a funnel-shaped structure within the polar nodule, and cytoplasm can pass from it into the terminal fissure and so into the outer fissure of the raphe.

It has been made highly probable that the raphe is in all cases occupied by streaming cytoplasm, which comes into direct contact with the external medium and constitutes the mechanism by which movement is brought about. In the Naviculoideae the cytoplasmic currents are in the same direction in the two parts of the raphe, viz. from terminal fissure to central nodule and again from central nodule to the other terminal fissure, whilst in the inner fissures the current is in the opposite sense. The existence of these currents has been demonstrated by placing cells in water containing sepia or suspended carmine.

[1] This structure exhibits a very varied differentiation and probably originated separately in different lines of evolution within the class. An abortion of the raphe on one valve in *Cocconeis* and *Achnanthes* is probable, but it is unlikely that the pseudo-raphe in all cases marks the former presence of a true raphe.

[2] cf. especially Müller, Ber. Deutsch. Bot. Ges. XIV, 1896, p. 54; XXVII, 1909, p. 27.

[3] Müller, Ber. Deutsch. Bot. Ges. VII, 1889, p. 169; XIV, 1896, p. 111.

In either case the particles are found to glide from the anterior (in the sense of the movement) polar nodule towards the central one where they exhibit a slight accumulation, to be subsequently projected backwards and outwards as a fine thread forming an acute angle with the valve (fig. 144, A, B)[1]. Frustules in motion are surrounded by a zone of soft mucilage which narrows to a point at the two ends of the individual, as well as at the central nodules. The thread just mentioned is regarded by Müller as due to agglutination of the sepia-particles by the mucilage, whilst Lauterborn interprets it as a special thread of denser mucilage to the excretion of which he would ascribe the actual cause of movement[2]. The very rapid movements of some Diatoms would however necessitate an excretion of mucilage at a rate and in such quantity as seems unbelievable. In view of the diversity of raphe-structure, it is not unlikely that the mechanism of movement may vary, but the balance of evidence seems in favour of cytoplasmic currents being a determining cause. In any case the older views attributing the movement to the passage of osmotic currents through the wall (Naegeli, Mereschkowsky) or to the protrusion of cilia or of a pseudopodium through the raphe (Ehrenberg, Cox, Bütschli) may now probably be dismissed.

In the numerous colonial freshwater Diatoms the frustules are connected by mucilage the secretion of which often takes place through readily recognisable pores (fig. 143, C and D). In the long filaments of *Melosira* (fig. 146, C), *Fragilaria* (fig. 152, D), etc. the frustules are joined by the faces of their valves, but in other cases they are united by mucilage-cushions at the corners, forming zig-zag colonies (e.g. *Tabellaria* (fig. 149, F)) or characteristic stellate groups (*Asterionella* (fig. 153)). In *Gomphonema* the frustules are attached by their narrower ends to a branched system of hyaline mucilage-stalks, epiphytic on various substrata, commonly the larger filamentous Algae. Some species of *Navicula* (*Frustulia*) and *Cymbella* (*Encyonema*) have large numbers of individuals enclosed in a common tubular mucilage-envelope which is sometimes branched, but this condition is more frequent in marine than in freshwater forms. A unique colonial type is the planktonic *Bacillaria paradoxa*, where the individuals of the ribbon-like colonies exhibit a peculiar gliding movement over one another.

[1] cf. especially Lauterborn, loc. cit. p. 115; Müller, Ber. Deutsch. Bot. Ges. xi, 1893, p. 571.

[2] With reference to this difference of opinion, see Lauterborn, Ber. Deutsch. Bot. Ges. xii, 1894, p. 73; Müller, ibid. p. 136, and xv, 1897, p. 70. Other recent literature dealing with Diatom-movements includes: Palmer, Proc. Delaware County Inst. Sci. v, 1910, p. 146 (see Bot. Centralbl. cxvii, 1911, p. 222).

The multiplication of Diatoms takes place generally at night, most commonly by successive bipartition. A slight increase in the volume of the frustule is followed by mitotic division of the nucleus[1] and a gradual fission of the protoplast from without inwards in a plane parallel to the valve-faces; thereupon new siliceous valves, at first very delicate, are formed over the fresh protoplasmic surfaces. The new valves are situated within the girdle of the parent-frustule, but as their connecting-bands develop, those of the parent separate. Thus each daughter-individual consists of a new and an old half, the connecting-band of the old valve overlapping that of the new. Since the valves when once mature are incapable of growth, one individual of each successive generation will tend to become reduced in size by the double thickness of a connecting-band. This statement is not strictly true, however, for some of the filamentous species and possibly not for many others. The new valves are often only slightly silicified and may undergo some increase in size before strong silicification sets in, so that the daughter-individuals may become larger than the parents; such are recognisable by the thickened rim of the valves. This has a retarding influence on the diminution in size of the frustules, hence this reduction is not in strict proportion to the number of divisions. Pure cultures of *Nitzschia Closterium* forma *minutissima* extending over two years showed no marked reduction in size[2]. Moreover, in the case of *Melosira arenaria*, Müller[3] has shown that division of the smaller daughter-cells is delayed as compared with the larger ones.

It has been thought that the other characteristic method of reproduction of Diatoms, by so-called *auxospores*, is conditional upon the individuals having reached a certain minimum size. Whilst this may well be a predisposing cause, especially in some forms, there are many facts that speak against its being of general application. For example, amongst pennate Diatoms forming their auxospores by conjugation (*Rhopalodia*, *Navicula*), the two individuals concerned are often of appreciably different dimensions. Nor is it likely that the factors determining auxospore-development are not in part environmental, as in the equivalent reproductive processes of other Algae[4].

The production of auxospores[5] takes place sexually in the

[1] Lauterborn, loc. cit. 1896, p. 60; van Wisselingh, Flora, cv, 1913, p. 265.

[2] Allen and Nelson, Journ. Marine Biol. Assoc. Plymouth, viii, 1910, p. 462.

[3] Jahrb. Wiss. Bot. xiv, 1884, p. 232.

[4] cf. especially Miquel, Ann. de Micrographie, v, 1893, p. 521, and x, 1898, pp. 49, 182; Le Microgr. préparateur, xi, 1903, pp. 84, 174.

[5] Useful synopses are given by Klebahn, Jahrb. Wiss. Bot. xxix, 1896, p. 599; Karsten, Biol. Centralbl. xx, 1900, p. 257.

Pennatae, but not in the Centricae, where however they are more often observed. A frequent method among Pennatae is that recorded for *Amphora ovalis* Kütz., *Navicula limosa* Kütz. (fig. 145, A), *Gyrosigma*, etc. and fully studied by Klebahn[1] in *Rhopalodia*. In this case two individuals come into close association, being united by mucilage in various ways; in each, two successive nuclear divisions ensue which presumably bring about chromosome-reduction, two of the resulting nuclei enlarging, whilst the other two diminish in size and sooner or later disappear. The protoplast of each individual divides at right angles to the long axis, the products round off and contract, the halves of the frustule separate, and the undifferentiated gametes fuse in pairs to form two auxospores (fig. 145, A). This process recalls the formation of double zygospores in some Conjugatae, although the cytological details are different.

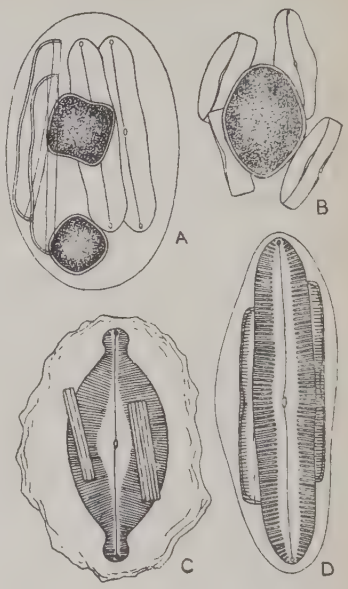

Fig. 145. A, *Navicula limosa* Kütz., from the New Forest, Hants (× 450). B, *Achnanthes flexella* (Kütz.) Bréb., from Craig-an-Lochan, Scotland (× 450). C, *Navicula Amphisbaena* Bory, from Barnes Common, Surrey (× 450). D, *N. viridis* Kütz., from Clough, Antrim, Ireland (× 350). A illustrates the first, B the second, C and D the third methods of auxospore-formation described in the text.

In *Surirella* and *Achnanthes flexella* (Kütz.) Bréb. (fig. 145, B) there is no division of the protoplast prior to conjugation, so that only one auxospore is produced. In the former, however, Karsten[2] demonstrated two nuclear divisions in each individual, the first of which brings about reduction; only one of the four nuclei persists. *Cocconeis* is similar, but here there is only one nuclear division. The conjugation-process[3] in this case is of interest because the gamete formed by one individual passes through a mucilaginous canal to fuse with the contracted protoplast of the other individual, an indication of physiological anisogamy comparable with that of *Spirogyra*.

Whilst in the cases as yet considered there is undoubted

[1] loc. cit. p. 595; cf. also Karsten, Flora, LXXXVII, 1900, p. 253.
[2] Zeitschr. f. Bot. IV, 1912, p. 417.
[3] Karsten, loc. cit. p. 254.

sexual fusion, this is not so in others which, judging by the little that is known of their cytology, are probably to be regarded as instances of apogamy. According to G. S. West (1916 *a*, p. 109) such production of auxospores without sexual fusion is much the commoner method. In *Achnanthes subsessilis* Kütz.[1] there is no approximation of individuals, but the protoplast divides into two uninucleate portions which subsequently again fuse to form a single auxospore. *Synedra affinis* Kütz. and *Achnanthes longipes* Ag. differ, inasmuch as each half of the protoplast gives rise to a separate auxospore without any fusion occurring. In *Navicula Amphisbaena* Bory (fig. 145, C), *N. viridis* Kütz. (fig. 145, D), and many others the protoplast of one of the smaller cells (enveloped in mucilage) swells up and escapes from the frustule as the auxospore, which is provided with a delicate membrane and rapidly increases in size; as the wall becomes silicified, the cell assumes an irregular form something like that of the parent. Here we have apparently merely a rejuvenescence of the protoplast accompanied by an increase in size, but, in the similar case of the marine *Rhabdonema adriaticum* Kütz., Karsten[2] demonstrated a nuclear division followed by degeneration of one of the nuclei (cf. *Cocconeis*)[3]. In *Cymbella* two frustules sometimes become enveloped in mucilage and throw off the old cell-walls, whereupon each protoplast rounds off and develops independently into an auxospore.

Among centric Diatoms formation of auxospores appears always to take place by rejuvenescence[4] of the protoplast which, pushing apart the two valves and increasing appreciably in size, rounds off as the auxospore (fig. 146, E); whether there are accompanying nuclear changes is at present unknown.

The auxospores in all cases sooner or later secrete a membrane (*perizonium*) which is composed of pectic substances and slightly silicified and within which the two halves of a new frustule are produced. The shape of the mature auxospores frequently approximates to that of the ordinary individual, but the first valves do not as a rule show all the characteristic markings of the species, which are usually only realised after a number of generations. There is at present no evidence that the auxospores represent resting-stages, and little is known as to the form in which most Diatoms persist from one period to another. Many are however capable of withstanding desiccation with little

[1] Karsten, Wiss. Meeresunters., Abt. Kiel, IV, 1899, p. 43.
[2] loc. cit. p. 33.
[3] cf. also Bachmann, Jahrb. Wiss. Bot. XXXIX, 1904, p. 130.
[4] Müller, Jahrb. Wiss. Bot. XLIII, 1906, p. 49; Ostenfeld, Proc. Roy. Soc. Edinburgh, XXV, 1906, p. 1116.

change other than a contraction of the protoplast into one corner of the cell[1]. True thick-walled resting-spores have been recorded in some species of *Melosira*, as well as in *Rhizosolenia* (fig. 148, C).

In a number of Pennatae the protoplast occasionally recedes from the wall and, without escaping, forms a pair of new valves; this may take place several times in succession, the valves often being abnormal in shape and in other respects. Such a *craticular state*, which has been interpreted as a resting condition, has been observed especially in the section *Himantidium* of the genus *Eunotia*, in *Fragilaria*, and in *Achnanthes*[2].

Subdivision of the protoplast to form a number of usually rounded *microspores*[3] has been recorded for *Eunotia lunaris* by Hustedt[4], for *Surirella spiralis*, where they are thick-walled, by G. S. West[5], and for a number of marine Centricae (e.g. *Corethron Valdiviae* Karst., *Chaetoceras decipiens* Cleve, *Biddulphia mobiliensis* Bail.). Their further fate remains in doubt. In the Centricae they are rounded naked cells which Karsten[6], in the case of *Corethron*, on rather slender evidence regards as motionless gametes. In *Biddulphia mobiliensis*, Bergon[7] reports the liberation of the naked microspores as swarmers with two laterally attached cilia, whilst in a marine *Coscinodiscus* Pavillard[8] records pear-shaped swarmers with two equal cilia at the front end, some possessing chromatophores being larger than others which are colourless. Non-motile microspores of two sizes have also been described in *Chaetoceras decipiens*[9]. The tendency is to regard all these structures in Centricae as gametes, but there is perhaps at present hardly enough evidence[10]. Should this view prove correct, the sexual reproduction of centric Diatoms would be of an altogether different type from that of Pennatae where it leads to the formation of auxospores, and the doubts that have

[1] Miquel, Ann. de Micrographie, IV, 1892, p. 328.

[2] Müller, Hedwigia, XXXVIII, 1899, p. 308, t. XI, fig. 17.

[3] These are scarcely comparable with the minute spores mentioned by Kitton (Journ. Quekett Microscop. Club, ser. 2, II, 1885, p. 178) and Lockwood (Journ. New York Micr. Soc. II, 1886, p. 153) which were described as being so small as to pass readily through filter papers.

[4] Abh. Nat. Ver. Bremen, XX, 1911, p. 275.

[5] West, 1912, p. 325.

[6] Ber. Deutsch. Bot. Ges. XXII, 1904, p. 544.

[7] Bull. Soc. Bot. de France, LIV, 1907, p. 327; cf. also Pavillard, Progr. Rei Bot. III, 1910, p. 542.

[8] Bull. Soc. Bot. de France, LXI, 1914, p. 167.

[9] Gran, Diat. d. arkt. Meere, in Römer u. Schaudinn, Fauna arctica, III, 1904, p. 536.

[10] cf. however Oltmanns, 1922, p. 193; Karsten, Rev. Hydrobiol. u. Hydrogr. XII, 1924, p. 116.

been felt as to the close relationship of the two series of Diatoms would receive substantial confirmation. The microspores observed in Pennatae are no doubt not homologous with those of the Centricae.

Diatoms are universally distributed in fresh and salt water, as well as in many terrestrial situations (incl. the soil itself, cf. Bristol, 1920). They often form a yellowish-brown scum at the surface, or a sediment at the bottom of the water, or thickly clothe larger Algae and other aquatic plants; characteristic epiphytes are *Cocconeis*, *Epithemia*, *Achnanthes*, species of *Synedra*, and *Gomphonema*. They also play a great rôle as Plankton-organisms[1] and in the ocean are more abundant than any other pelagic plants. They are most numerous in cold latitudes, having a decided preference for cold water, although some have become adapted to life in hot springs. Mountainous regions generally have a rich Diatom-flora. They usually exhibit a marked periodicity[2], which Pearsall[3] has shown often to be related to the occurrence of flood conditions whereby the nitrate and silica content of the water is increased.

Diatoms form a considerable part of the food of many fresh-water and marine animals and are often found in quantity in the alimentary tracts of Molluscs, Crustacea, Tunicates, and Fishes. They also occur in abundance in guano, having passed through the digestive systems of birds feeding on marine animals. Some of the freshwater species (especially *Asterionella*) are occasionally the cause of foulness in drinking water, owing to the escape from the dead frustules of an oil produced within the cells[4].

Large numbers of fossil Diatoms are known. Not only are these minute plants actively engaged at the present time in forming oceanic (especially in the Arctic and Antarctic oceans) and lacustrine deposits, but similar *Diatomaceous earths*[5] (Kieselguhr), found principally associated with rocks of Tertiary age, are a proof of their activities in former eras. Such earths are of a white or grey colour, often so soft and friable as to crumble

[1] Whilst in the sea the dominant Plankton-Diatoms are centric, pennate forms (e.g. species of *Tabellaria*, *Asterionella*, *Synedra*, *Fragilaria*, *Surirella*) are more abundant in freshwater plankton, although some centric forms are frequent (e.g. *Melosira*, *Cyclotella*, *Rhizosolenia*).

[2] Fritsch and Rich, 1909, p. 42; Fritsch and Rich, 1913, p. 55; West and West, 1912.

[3] Journ. of Ecol. XI, 1923, p. 165.

[4] Whipple, Trans. Amer. Micr. Soc. XXII, 1901, p. 35; Moore, Yearbook U.S. Depmt. Agric. 1902, p. 182.

[5] cf. West, 1911, p. 83; Henderson, Trans. Bot. Soc. Edinburgh, XXIX, 1925, p. 135; West, Journ. of Bot. 1912, p. 79; Fritsch and Rich, Trans. Roy. Soc. S. Afr. XII, 1925, p. 277. The last two deal with recent deposits.

readily between the fingers, and they are composed almost entirely of the siliceous valves of Diatoms. Most of the forms present belong to genera, and many of them to species, now living. Some of the deposits are of economic importance, being used as polishing powders ("Tripoli"), as non-conducting materials, in the manufacture of dentifrices, as absorbents for nitro-glycerine in the manufacture of dynamite, etc. Although many species usually occur in such earths, one is mostly predominant. The best-known deposits in the British Islands are those at Dolgelly in Wales and at Toome Bridge in Antrim, Ireland. That at Bilin in Bohemia, which averages 14 ft. in thickness, was estimated by Ehrenberg to contain some 40,000,000 frustules in every cubic inch[1]. That at Richmond, Virginia, U.S.A., is very extensive and reaches a thickness of 30 ft., whilst on some of the geological surveys in the western states of America beds have been discovered no less than 300 ft. thick and containing on an average 80 per cent. of silica.

The earliest appearance of fossil Diatoms seems to be in the Trias (Kusnetzk in Hungary). Castracane recorded the occurrence of certain species in coal from the English Carboniferous beds, a statement that has never been confirmed and is doubtless incorrect[2].

The affinities of Diatoms are obscure. There are undoubted resemblances to the Desmidiaceae, but they are purely superficial, as is very apparent on closer consideration. On the other hand, Bacillariales resemble Heterokontae and Chrysophyceae in a preponderance of yellow or brown pigments in the chromatophores, in the absence of starch, in the usual occurrence of oil as an assimilatory product, and in certain features of the cell-membranes. Pascher[3] has drawn attention to the resemblance between the cell-wall structure of Diatoms possessed of numerous intercalary bands (e.g. *Rhabdonema*) and that of an *Ophiocytium* or *Tribonema* (cf. p. 298) or the envelope of various Chrysophyceae (*Dinobryon*, etc., p. 318). The cysts of Heterokontae and Chrysophyceae resemble the ordinary Diatom-individual in their silicification and the bipartite character of their membranes; moreover the endogenous cysts of the marine plankton Diatom *Chaetoceras* show many points of structural similarity with those of various Chrysomonadales. If swarmers occur in Diatoms

[1] Brandt (Wiss. Meeresunters., Abt. Kiel, III, 1898, p. 78) states that 675,000,000 of the dried frustules of Diatoms (mostly *Chaetoceras*) weigh one gramme.

[2] cf. Seward, Fossil Plants, I, 1898, p. 154.

[3] Pascher, 1921, p. 236.

there is a further point of contact. Pascher considers the resemblances sufficiently significant to warrant the assumption of a common origin. He suggests the establishment of a group Chrysophyta to include Heterokontae, Chrysophyceae, and Bacillariales, the latter being supposed to occupy much the same position in this group as do the Conjugatae among the green Algae (Pascher's Chlorophyta). His point of view is certainly a stimulating one.

The classification of Diatoms is founded solely on the characters of the cell-wall. This applies not only to the larger groups, but also to the genera and even to species. It appears certain that the features presented by the cell-contents can never afford a basis for the distinction of families or genera, but the characters of the chromatophores[1] may well help in generic diagnosis and may in some cases be of considerable specific importance. Much reliance in specific distinction is placed on the number and exact arrangement of the striae (whether parallel, divergent, or convergent at certain points on the valves) and, whilst this is undoubtedly very constant within certain limits, there has been a tendency in certain quarters to drive it to an extreme. It is well to remember that Héribaud[2] has shown that increased altitude and enfeebled light cause a diminution in the number and strength of the striae, accompanied by an increase in the length and breadth of the valves.

In the earlier edition of this work the classification of Diatoms proposed by Schütt[3] was adopted with a few slight modifications. Later G. S. West (1916 *a*, p. 123) suggested a classification founded partly on that of Schütt and partly on one put forward by Forti[4]. The latter is essentially based on the non-occurrence or occurrence of movement and the formation of auxospores without or with conjugation (Immobiles and Mobiles respectively). The present writer has, however, been reluctant to depart from the arrangement formerly adopted, which is considered more probably to represent a natural system. This classification[5] is as follows:

[1] Various classifications, based upon the disposition and mode of division of the chromatophores, are impracticable, alone because so many genera and species are unknown in the living state: cf. for instance Pfitzer, Hanstein's Bot. Abh., Heft 2, 1871, p. 151; Petit, Bull. Soc. Bot. France, XXIII, 1876, p. 372; Ott, Sitz.-Ber. Akad. Wiss. Wien, Mat.-nat. Kl. CIX, 1900, p. 769.

[2] Comptes Rendus, CXVIII, 1894, p. 82.

[3] Engler-Prantl, Nat. Pflanzenfam., Teil 1, Abt. 1 *b*, p. 55.

[4] Atti R. Ist. Veneto, LXXI, 1912, p. 677.

[5] Various excellent works for the determination of Diatoms exist. The student is referred especially to: W. Smith, A synopsis of the British

A. *Centricae.* Valves radially symmetrical about a central point, without raphe or pseudo-raphe; valve-view circular, polygonal, or broadly elliptical, rarely boat-shaped or irregular. No movement. Auxospores formed without conjugation.

Series I. *Discoideae.* Cells shortly cylindrical or disc-shaped; valves circular, hyaline, areolated, or with radiating striations.

Series II. *Solenoideae.* Cells elongate, cylindrical or subcylindrical, circular or broadly elliptical in cross-section (or in the valve-view); girdle complex, with a considerable development of intercalary bands, giving the frustules a scaly structure; apices of frustules often obliquely conical and furnished with a spine.

Series III. *Biddulphioideae.* No British freshwater representatives[1].

Series IV. *Rutilarioideae.* No British freshwater representatives.

B. *Pennatae.* Valves isobilateral, medianly zygomorphic, or less frequently dorsiventral, never centric; valve-view mostly boat- or needle-shaped, with a structure arranged in relation to a raphe or pseudo-raphe (sagittal axis). Movement in many forms. Auxospores formed with or without conjugation.

Series I. *Fragilarioideae.* Valves mostly straight, rod-shaped or lanceolate, without a raphe, but usually with a pseudo-raphe, or showing indications of a rudimentary raphe.

Series II. *Achnanthoideae.* Frustules crooked or suddenly bent in the girdle-view; with a raphe and nodules on one valve, a pseudo-raphe on the other.

Series III. *Naviculoideae*[2]. Each valve with a raphe, central and polar nodules; valves rarely keeled in the line of the raphe (sagittal axis).

Series IV. *Nitzschioideae*[2]. Each valve with a raphe, which is situated in a keel with carinal dots. Keels of the two valves situated on opposite sides of the frustule or displaced to the same side. No nodules. Cells rhombic in transverse section.

Series V. *Surirelloideae.* Cells with two raphes, without nodules, in the two marginal wings of each valve; sagittal axis of each valve occupied by a pseudo-raphe; valves strongly costate.

Diatomaceae (1853–56); Van Heurck, Synopsis des Diatomées de Belgique (Anvers, 1880–85); Cleve, Synopsis of the Naviculoid Diatoms (K. Sv. Vet.-Ak. Handl. xxvi, No. 2, 1894, and xxvii, No. 3, 1895); Meister, Kieselalgen der Schweiz (Bern, 1912); v. Schönfeldt, Bacillariales, in Pascher, Süsswasserflora Deutschlands, Österreichs, u. der Schweiz (Jena, 1913); Schmidt, Atlas der Diatomaceenkunde (Leipzig, 1874 and onwards).

[1] The interesting *Attheya Zachariasi* J. Brun (Forschungsber. Biol. Stat. Plön, II, 1894, p. 52), recorded in the plankton of various continental freshwaters, has so far not been found in the British Isles.

[2] These two series are not distinguished in Schütt's scheme. Forti's Immobiles include all the Centricae and the Fragilarioideae, with the exception of the Eunotiaceae.

GROUP A. CENTRICAE

This includes a relatively small proportion of the known species of Diatoms and few are inhabitants of freshwater. The cells of these are commonly cylindrical, sometimes discoid, and the valves are circular and not uncommonly provided with spines. Many occur as solitary, free-floating individuals, but others are joined by their valve-faces to form filaments. The markings on the valves are either concentrically disposed or take the form of radiating striae, the latter often terminating in marginal punctulations or dots. In all cases the markings are arranged in relation to a centre and never in relation to a middle line. There is no raphe or pseudo-raphe. There are usually many small parietal chromatophores of a plate-like form, but occasionally only two large plates are present. Auxospores are known only in a few species.

The following key will facilitate the determination of the British freshwater genera:

I. Cells shortly cylindrical or discoid, valves circular *Discoideae*

A. Cells subspherical or shortly cylindrical, united to form long filaments, girdle usually with a fine sculpturing *Melosiraceae*

Only genus *Melosira*

B. Cells mostly disc-shaped and usually solitary, girdle mostly structureless *Coscinodiscaceae*

a. Marginal portions of valves striate, the centre smooth or granulate *Cyclotella*

b. Marginal and central portions of valves not sharply delimited

1. Valves with marginal spines *Stephanodiscus*

2. Valves with submarginal spines and a differentiated edge *Coscinodiscus*

II. Cells elongate, cylindrical or subcylindrical, valves circular or broadly elliptical, girdle with numerous scaly intercalary bands *Solenoideae*

Only family *Rhizosoleniaceae*

A. Frustules asymmetrical, valves with an excentric apical spine *Rhizosolenia*

B. Frustules spindle-shaped, symmetrical, apically attenuated *Cylindrotheca*

Series I. DISCOIDEAE

Family 1. MELOSIRACEAE

A family in which the individuals are usually united to form long filaments. The only freshwater genus is

Melosira Agardh, 1824[1] (*Orthosira* Thwaites; *Sphaerophora* Hassall). Frustules usually cylindrical, rarely ellipsoidal or globular, united by gelatinous cushions or a peripheral ring of small spines or teeth to form filaments of variable length. Valves flat or convex, rarely strongly arched, the circular valve-faces often divided into differently marked central and peripheral regions (fig. 146, A). Girdle-view rectangular, the girdle frequently provided, except at its middle, with longitudinal striations or systems of punctae; in the region of the smooth part of the girdle the frustules commonly show one or two annular constrictions or internal ridge-like projections of the membrane.

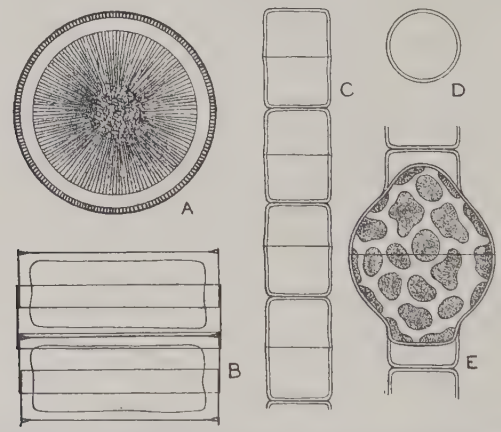

Fig. 146. A and B, *Melosira arenaria* Moore, from Shipley Glen, W. Yorks. C–E, *M. varians* Ag., from the River Cam at Cambridge; E, showing formation of auxospore. (All ×450.)

Chromats. small, numerous, parietal, and plate-like. Auxosp. formed by rejuvenescence of the protoplast, much larger than the parent-cell, the long axis either parallel or at right angles to that of the latter; auxosp. commence to divide while still part of the original filament.

The freshwater sp. are generally grouped in two sections, viz. *Melosira* proper where marginal spines are lacking, and *Orthosira* where they are present. To the former belongs *M. varians* Ag., to the latter *M. arenaria* Moore, *M. granulata* (Ehrenb.) Ralfs, and *M. Roeseana* Rabenh.

There are some six or eight freshwater sp. in the Brit. Isles. *M. varians* Ag. (fig. 146, C–E) is one of the most abundant centric Diatoms, occurring in large quantities in ponds, ditches, and slow

[1] Müller, Jahrb. Wiss. Bot. XIV, 1884, p. 232, and XLIII, 1906, p. 49; Müller, Ber. Deutsch. Bot. Ges. XXI, 1903, p. 326.

rivers; the frustules (15–35 br.) are almost devoid of markings, presenting only a very fine punctation. *M. arenaria* Moore (fig. 146, A, B) occurs on wet rocks, sometimes forming crisp mat-like masses on dripping sandstone, and is common on the Brit. Carboniferous sandstone; the greater part of the girdle shows a fine cross-hatching; valves 40–90 br. *M. granulata* (Ehrenb.) Ralfs, with elongate frustules (5–20 br.) and a coarsely punctate girdle, occurs in boggy pools and in the plankton. *M. Roeseana* Rabenh., in which the centre of the valve has 3–5 strong punctae, is found on damp rocks among various Myxophyceae and also among damp Mosses. Schröder[1] has described a greenish iridescence due to specimens of the last-named sp. growing in a cave.

Family 2. COSCINODISCACEAE

In this family the usually discoid cells are generally solitary. The circular valves are flat, convex, or more rarely arched, and they are sometimes provided with a peripheral ring of spines. They commonly show radial rows of punctulations or areolations, but the girdle is mostly structureless. The small and numerous chromatophores are rounded or lobed parietal plates. The auxospores are formed by rejuvenescence of the protoplast. Most of the members of this family are marine or fossil.

Cyclotella Kützing, 1833[2]. Frustules solitary or paired, rarely in chains, disc-shaped. Valves circular, very rarely elliptical, exhibiting two concentric areas (fig. 147, B), the inner smooth or granulate, the outer with smooth or punctate radiating striae, occasionally with minute spines near the margins; valves excentrically bullate in most sp., so that the girdle-view possesses undulate margins (fig. 147, C).

Of the six sp. known to occur in Brit. freshwaters, *C. operculata* Kütz. (fig. 147, B, C), *C. Meneghiniana* Kütz. with coarser striations, and *C. Kützingiana* Thw. are more or less widely distributed. *C. comta* (Ehrenb.) Kütz., in which some of the striae are coarser than others, is often abundant in the plankton. The colonial *C. Schröteri* Lemm. (*C. comta* var. *quadrijuncta* Schröt.), in which the frustules are held together within mucous tubes, is known from the plankton of Lough Corrib, Galway (West and West, 1906, p. 108). The valves of these different sp. vary from 10–30 br.

Stephanodiscus Ehrenberg, 1845. Frustules solitary, disc-shaped. Valves circular, with a marginal ring of simple acute spines; valve-faces with radiating series of punctulations, alternating with radiating smooth spaces which appear as lines;

[1] Ber. Deutsch. Bot. Ges. xxxiv, 1916, p. 796.

[2] Lemmermann, Ber. Deutsch. Bot. Ges. xviii, 1900, p. 29; Bachmann, Jahrb. Wiss. Bot. xxxix, 1904, p. 106.

centre of valves sometimes bullate, with punctulations more or less in line with the marginal ones.

S. Hantzschianus Grun. (fig. 147, A), one of the two Brit. sp., occurs in the plankton of Lough Neagh and of the Thames and has also been recorded from a Berkshire pool; the frustules (diam. 12–20) are sometimes provided with long siliceous needles. The markings on the valves are very hard to see.

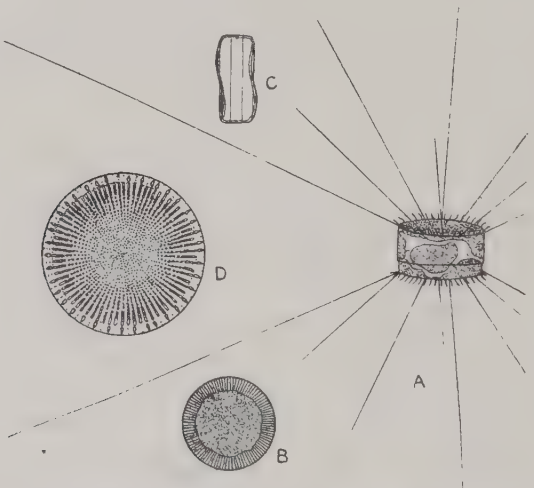

Fig. 147. A, *Stephanodiscus Hantzschianus* Grun. (after Schröder, ×544). B and C, *Cyclotella operculata* Kütz., from Shipley Glen, W. Yorks (×450). D, *Coscinodiscus lacustris* Grun., from the plankton of Lough Neagh, Ireland (×450).

Coscinodiscus Ehrenberg, 1838. Frustules solitary. Valves circular or rarely elliptical, with a differentiated edge, usually furnished with a ring of submarginal spines and, within the edge, radiating punctulations or areolations. Chromats. numerous, rounded, closely crowded.

The limits of this genus are exceedingly difficult to define. There are over 300 known sp., mostly marine, and the only Brit. freshwater sp. is *C. lacustris* Grun. (fig. 147, D) found in the still waters of rivers and lakes (sometimes in the plankton); it reaches a diam. of 60 μ.

Series II. SOLENOIDEAE

Family RHIZOSOLENIACEAE

The frustules, which are sometimes imperfectly silicified, are elongated and more or less cylindrical, with a circular or broadly elliptical cross-section or valve-view; they sometimes occur in

chains. The extremities of the cells are attenuated and either symmetrical or asymmetrical. The girdle comprises numerous rhomboidal imbricating intercalary bands that give it a scaly appearance.

Rhizosolenia Ehrenberg, 1858; emend. Peragallo, 1892[1]. Frustules feebly silicified, very elongate, subcylindrical, often forming chains. Valves asymmetrical, calyptra-like, terminating

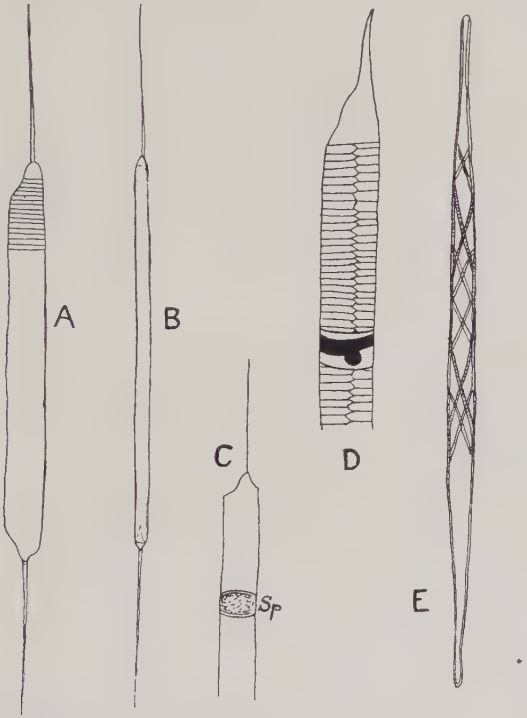

Fig. 148. A–C, *Rhizosolenia morsa* W. & G. S. West (after W. & G. S. West); A and B, from the Irish plankton (×375); C, individual with resting-spore (*Sp*), from the plankton of Thirlmere, Scotland (×320). D, *Rhizosolenia eriensis* H. L. Smith (after Ostenfeld & Wesenberg-Lund). E, *Cylindrotheca gracilis* (Bréb.) Grun. (after Van Heurck, ×360).

in an excentric spine or long seta parallel to the long axis of the cell. Intercalary bands numerous, scaly, often transversely extended and more or less imbricate (fig. 148, D). Chromats. small rounded or oval plates. Thick-walled resting-spores,

[1] Peragallo, Diatomiste, I, 1892, p. 108; West and West, 1906, p. 109; Bachmann, 1907, p. 74; Schröder, Ber. Deutsch. Bot. Ges. XXIX, 1911, p. 739.

pointed at one end and rounded at the other, arise to the number of one or two in a cell.

Most sp. are marine, but three are known to occur in the Brit. freshwater plankton. One of the commonest is *R. morsa* W. & G. S. West (*R. eriensis* H. L. Smith var. *morsa* W. & G. S. West (fig. 148, A–C)) in which the valves bear a relatively coarse spine and exhibit a characteristic excavation in the girdle-view. *R. longiseta* Zach., with very long setae, occurs in the Scottish plankton, whilst *R. eriensis* Sm. (fig. 148, D) has been recorded from Loch Shin.

Cylindrotheca Rabenhorst, 1859. Frustules symmetrical and spindle-shaped, with the apices much attenuated, ornamented with several spiral lines running from end to end and crossing one another at intervals. Chromats. small, granular.

The structure of the wall is only imperfectly known and the position of the genus is uncertain; it should perhaps be associated with the Nitzschiaceae. *C. gracilis* (Bréb.) Grun. (*Nitzschia Taenia* Sm. (fig. 148, E)), the only known sp., occurs rarely in English fresh and brackish waters; frustules 5–9 br.

GROUP B. PENNATAE

These include the majority of Diatoms. The markings (striae or costae) on the valves are usually arranged on either side of a sagittal line (which is occupied by a raphe or pseudo-raphe) and not in relation to a central point. The frustules are most commonly naviculoid or boat-shaped, but they may have the form of a flattened plate or an elongated rod, and may be straight, arcuate, or sigmoid. They are never cylindrical, and there is a striking absence of spines and long processes. The different forms exhibit all degrees of development of the raphe which reaches its highest differentiation in the Naviculoideae, whilst in the Nitzschioideae it is situated on a median or obliquely disposed keel. The chromatophores are always parietal; in the lower series each cell contains a large number of small plates, but in the higher one a few large lobed chromatophores occupy the greater part of the inner surface of the cell-wall. The auxospores are formed by conjugation or apogamously.

The following key will serve to identify the British freshwater genera:

I. Cells rod-shaped, lanceolate, cuneate, or arcuate in valve-view, rectangular in girdle-view, mostly with a pseudo-raphe or traces of a true raphe *Fragilarioideae*

A. Frustules stout, tabular in girdle-view, usually united to form band-like or zig-zag colonies, with two or more well-developed

longit. septa internally; valves bilaterally symmetrical, with or without a median pseudo-raphe *Tabellariaceae*

a. Frustules without transv. septa

1. Valves without transv. ribs

* Longit. septa often numerous, as short plates arising alternately on the two sides of the girdle, valves swollen in the middle and at the apices *Tabellaria*

** Longit. septa two, perforated by three foramina, valves only swollen in the middle *Diatomella*

2. Valves with transv. ribs, longit. septa with a single median foramen *Tetracyclus*

b. Frustules with two longit. and a number of transv. septa, appearing as capitate ribs in the girdle-view *Denticula*

B. Frustules cuneate, with transv. septa only, united to form flat spiral colonies; valves clavate, with an indistinct median pseudo-raphe *Meridionaceae*

Only freshwater genus *Meridion*

C. Frustules rectangular, without longit. septa, united into band-like or zig-zag colonies; valves rod-shaped or lanceolate, with transv. septa *Diatomaceae*

Only genus *Diatoma*

D. Frustules rectangular, without septa, often united to form ribbon-like colonies; valves lanceolate or rod-shaped with a median pseudo-raphe *Fragilariaceae*

a. Valves equally developed at both ends, frustules solitary or colonial

1. Ribbon-like colonies *Fragilaria*

2. Solitary or as attached radiating clusters *Synedra*

b. Valves more swollen at one end than at the other, frustules forming star-shaped colonies *Asterionella*

E. Frustules solitary or in band-like colonies; valve-view slightly curved or arcuate, pseudo-raphe nearer to one edge of valve *Eunotiaceae*

a. Valves with a median swelling on their concave (ventral) surface *Ceratoneis*

b. Valves without such a swelling, the dorsal margin often undulate *Eunotia*

II. Girdle-view crooked or suddenly bent, sometimes cuneate, with a true raphe on one and a pseudo-raphe on the other valve *Achnanthoideae*

Only family *Achnanthaceae*

a. Girdle-view not cuneate

1. Valves lanceolate or rod-shaped, frustules generally occurring as stalked epiphytes *Achnanthes*

2. Valves subcircular or broadly elliptical, frustules epiphytic by their flat faces *Cocconeis*

b. Girdle-view cuneate, valves somewhat clavate *Rhoicosphenia*

III. Each valve with a true raphe, with a central and two polar nodules, valves rarely keeled *Naviculoideae*

A. Valves straight, rarely oblique or sigmoid, generally with a straight raphe, more rarely with an oblique one, mostly symmetrical about the line of the raphe and about a transv. axis; girdle-view usually rectangular *Naviculaceae*

a. Frustules without septa

1. Valves straight and symmetrical; raphe straight

* Central nodule mostly small and rounded *Navicula*

** Central nodule transv. distended to form a stauros *Stauroneis*

*** Central nodule linear and greatly elongated in the sagittal axis *Amphipleura*

2. Valves sigmoid; raphe sigmoid *Gyrosigma*

3. Valves naviculoid, with a sigmoid keel containing the raphe, frustules twisted *Amphiprora*

b. Frustules with two longit. perforated septa and radially arranged chambers along each margin of the valve *Mastogloia*

B. Valves mostly straight and symmetrical about the line of the raphe, with one pole larger than the other; girdle-view wedge-shaped; epiphytes *Gomphonemaceae*

Only genus *Gomphonema*

C. Valves always curved, often sublunate, symmetrical only about a transv. plane; girdle-view straight, subrectangular or elliptic *Cymbellaceae*

a. Valves without transv. ribs

1. Valves flat, not very asymmetrical; raphe removed from the edge of the girdle which is without striae *Cymbella*

2. Valves crested, strongly asymmetrical; raphe very near edge of girdle on concave side; girdle with longit. striations *Amphora*

b. Valves with transv. ribs

1. Valves somewhat convex, raphe much curved and often conspicuous, near the ventral surface *Epithemia*

2. Valves crested, raphe in apex of crest (apparently on dorsal side) *Rhopalodia*

IV. Each valve with a raphe situated in a keel with carinal dots; no nodules; frustules rhombic in transv. section *Nitzschioideae*

Only family *Nitzschiaceae*

a. Keel median; cells joined to form loose ribbons *Bacillaria*

b. Keel displaced to one side; cells solitary

1. Keels of the two valves diagonally opposite *Nitzschia*

2. Keels of the two valves on the same girdle-face *Hantzschia*

V. Each valve with a pseudo-raphe and spreading marginal wings, containing a simple raphe (two to each valve), without nodules; valves often strongly costate *Surirelloideae*

Only family *Surirellaceae*
a. Valve-faces distinctly undulate *Cymatopleura*
b. Valve-faces not undulate
1. Valves elliptical, linear, or ovate, rarely twisted, with strong transverse ribs; pseudo-raphe of one valve parallel to that of the other *Surirella*
2. Valves circular, frustules saddle-shaped; pseudo-raphe of one valve at right angles to that of the other *Campylodiscus*

Series I. FRAGILARIOIDEAE

Family 1. TABELLARIACEAE

In this family the valves are bilaterally symmetrical, linear or linear-elliptic, often with a swollen median portion and sometimes with subcapitate extremities; the two valves are precisely similar and may have a straight median pseudo-raphe. The frustules are stout and appear as flat rectangular plates in the girdle-view; intercalary bands are developed and from these arise two or more incomplete longitudinal septa running parallel to the valve-faces. The frustules are mostly united to form band-shaped or zig-zag colonies (fig. 149, F) by mucous cushions on the valve-faces or at the corners. The chromatophores are numerous and granular.

Tabellaria Ehrenberg, 1839. Frustules tabular, united to form zig-zag colonies, the basal cell often fixed to a substratum by a mucous cushion at one corner. Longit. septa two or many, arising alternately on the two sides of the girdle and not reaching the centre; in the girdle-view these appear as prominent lines, and between them, as well as on the middle part of the girdle, there are fine striations. Valves sublinear, more or less strongly swollen in the middle and subcapitate at the ends, transv. striated, the striations interrupted by an indistinct median pseudo-raphe which is broadened in the middle and at the ends. Two auxosp. formed from each mother-cell.

There are two common Brit. sp., of which *T. flocculosa* (Roth) Kütz. (fig. 149, F, G), with numerous septa, is the most abundant. *T. fenestrata* (Lyngb.) Kütz. (figs. 143, D; 149, D, E) has fewer septa and more slender and elongate valves, the largest specimens reaching a length of 137 μ. *T. fenestrata* var. *asterionelloides* Grun., in which the frustules exhibit a stellate arrangement, is general in the plankton of all the Brit. lake areas, and there are two very distinct forms of it. Bachmann (1907, p. 68) has shown that the two sp. of *Tabellaria* are connected by transitional forms.

Diatomella Greville, 1855[1]. Frustules tabular, solitary, or joined to form ribbon-like colonies. Longit. septa two, visible in the valve- and the rectangular girdle-view, extending right across the frustule, and perforated by one central and two polar foramina. Valves oblong-lanceolate, sometimes with a slight median swelling, transv. striated, with indications of a pseudo-raphe and traces of nodules.

D. Balfouriana Grev. (fig. 161, E–F, p. 378), the only sp., is a rare British montane form; valves 30 l.

Tetracyclus Ralfs, 1843; emend. Grunow, 1862[2]. Frustules tabular, united to form short or long ribbons. Longit. septa

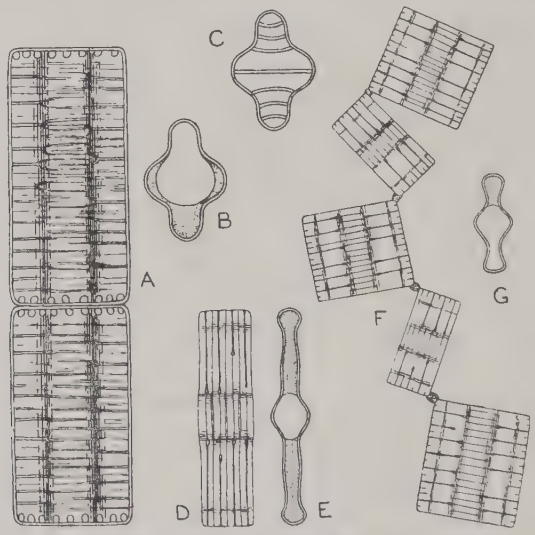

Fig. 149. A–C, *Tetracyclus lacustris* Ralfs, from the plankton of Loch Shin, Sutherland. D and E, *Tabellaria fenestrata* (Lyngb.) Kütz., from Mickle Fell, N. Yorks. F and G, *T. flocculosa* (Roth) Kütz., from the same locality. (All × 500.)

several, with a single, not absolutely median, foramen (fig. 149, B), appearing in the girdle-view as ribs with thickened apices. Valves elongate elliptical, with or without a median swelling, with few or many transv. ribs which appear as marginal teeth in the girdle-view; no pseudo-raphe.

There are two Brit. sp. *T. lacustris* Ralfs (valves up to 30 l.) (fig. 149, A–C) prefers hilly districts and is often found in the plankton of

[1] cf. Carter, Journ. Linn. Soc., Bot. XLVI, 1922, p. 56.
[2] Hustedt, Abh. Nat. Ver. Bremen, XXIII, 1914, p. 90.

mountain lakes. *T. rupestris* (A. Br.) Grun., with valves not swollen in the middle, occurs on dripping rocks in mountainous areas.

Denticula Kützing, 1844. Frustules more or less tabular, solitary, or forming short filaments. Longit. septa two, each with a row of perforations. Valves lanceolate with carinate faces, with transv. septa appearing in the valve-view as strong ribs (between which are delicate punctate striae) and in the subrectangular girdle-view as capitate marginal ribs; the transv. septa are fused with the edges of the perforations in the adjacent longit. septum; no pseudo-raphe.

The genus includes *Denticula* proper with transv. ribs extending right across the valves, and *Grunowia* in which they are confined to one half and which is often referred to *Nitzschia*. To the former belong: *D. tenuis* Kütz. (fig. 150, C and D) and *D. elegans* Kütz., with more widely spaced ribs, both frequent among Mosses on wet or dripping rocks; valves up to 45 l. *D.* (*Grunowia*) *sinuata* W. Sm., with valves having undulate margins, is frequent in the same localities.

Family 2. MERIDIONACEAE

The frustules are elongate and cuneate in both valve- and girdle-views and are therefore zygomorphic, being symmetrical only in relation to the longitudinal axis. They are either united

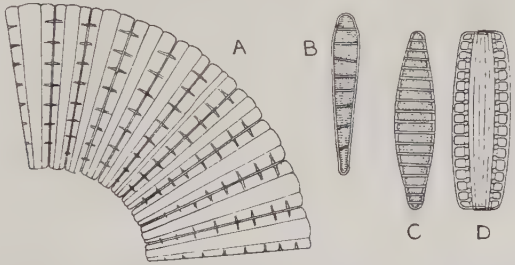

Fig. 150. A and B, *Meridion circulare* (Grev.) Ag., from Shipley Glen, W. Yorks (×500). C and D, *Denticula tenuis* Kütz., from Wicken Fen, Cambridge (×600).

by their valve-faces to form a flat spiral filament (*Meridion* (fig. 150, A)) or disposed at the extremities of a branched system of gelatinous stalks (*Licmophora*, marine only). In the marine forms there are two or more longitudinal septa, but none in *Meridion*, which however has short transverse septa. There is an indistinct pseudo-raphe. The chromatophores are small, plate-like, and numerous. Two auxospores arise from two mother-cells.

Meridion Agardh, 1824. Frustules cuneate, remaining attached after division to form flat, fan-shaped or spiral, free-floating filaments, often making two complete turns. Valves

clavate, sometimes with a subcapitate apex, with a number of continuous transv. costae, between which are fine punctate striae interrupted in the middle by a more or less distinct pseudo-raphe. Girdle-view cuneate, with a truncate base and apex. No longit. septa, but a number of transv. septa appearing as very short ribs in the girdle-view and as the transv. costae of the valve-view.

Except for their shape, the frustules show much similarity with those of *Diatoma*[1]. *M. circulare* Ag. (fig. 150, A, B), the only Brit. sp., is often abundant in stagnant ditches and ponds, and may frequently be obtained in pure masses. The var. *constrictum* (Ralfs) Van Heurck (sometimes regarded as a distinct sp.), in which the valves have subcapitate apices, is also frequent, being most abundant in early spring and often forming brown flocculent masses around submerged grass-leaves, etc.; valves 25–45 l.

Family 3. DIATOMACEAE

Another family of colonial forms, only represented in fresh-waters by the genus

Diatoma De Candolle, 1805. Frustules rectangular, united to form ribbon-like or zig-zag filaments. Valves without a keel, isobilateral, rod-shaped or lanceolate, sometimes with capitate

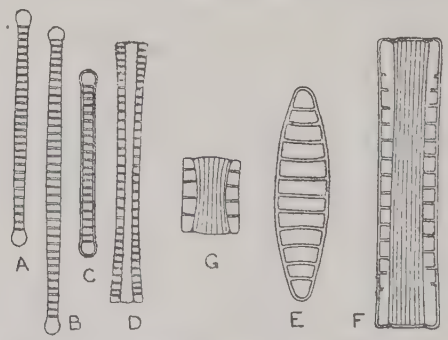

Fig. 151. A–D, *Diatoma elongatum* Ag., from Wicken Fen, Cambridge. E and F, *D. hiemale* (Lyngb.) Heib., from Howgill Fells, W. Yorks. G, *D. hiemale* var. *mesodon* (Kütz.) Van Heurck, associated with the typical form. (All × 500.)

extremities, with transv. ribs between which are fine punctate striae; pseudo-raphe indistinct. Longit. septa absent or as mere traces; the strongly marked transv. septa appear as ribs in the

[1] Forti (loc. cit. p. 726) classes *Denticula*, *Diatoma*, *Meridion*, and *Asterionella* in one family (Diatomeae), the other three genera of Tabellariaceae being placed among his Tabellarieae.

valve-view and are more or less distinct in the girdle-view. Chromats. small granules.

This genus is distinguished from *Denticula*[1] by the absence of a keel on the valve-faces and of longit. septa. There are four Brit. sp., of which *D. vulgare* Bory with more or less lanceolate valves (40–50 l.), *D. elongatum* Ag. (fig. 151, A–D; valves up to 70 l.), and *D. hiemale* (Lyngb.) Heib. (fig. 151, E, F) are common; the two former are very variable and possess zig-zag colonies, whilst in the last they are band-shaped. The first two sp. are generally distributed in quiet waters, but the last-named is more abundant in hilly districts, often occurring in pure masses or mixed with a smaller variety (var. *mesodon* (fig. 151, G)).

Family 4. FRAGILARIACEAE

In this family the frustules are solitary, or joined to form ribbon-like or zig-zag colonies, or they are arranged in a stellate manner. The elongate rod-shaped or lanceolate valves are isobilateral, not keeled, and there is usually an evident pseudo-raphe, sometimes with slight traces of central and polar nodules. There are no ribs on the valves and no septa. The chromatophores are sometimes small and granular, or they may be in the form of large plates.

Fragilaria Lyngbye, 1819 (*Odontidium* Kützing, pro parte; *Grammatonema* Kützing; *Ralfsia* O'Meara). Frustules rectangular, joined by their valve-faces to form ribbons or more rarely united by small mucous cushions at their corners to form zig-zag colonies. Valves fusiform, lanceolate, or linear, generally with produced apices, and sometimes with one or two inflations, with transv. striations which may be exceedingly fine, or rather coarse and composed of bead-like punctulations; pseudo-raphe sometimes scarcely evident (*Eufragilaria* Ralfs), sometimes broad (*Staurosira* Ehrenb. = *Odontidium* Kütz.); no nodules. Girdle-view rectangular. Chromats. small and granular (*Eufragilaria*) or one, two, or four plate-like bodies with pyrenoids (*Staurosira*).

Of the five Brit. sp., *F. capucina* Desmaz. (fig. 152, C and D; valves 30–60 l.) is much the commonest, but *F. mutabilis* (W. Sm.) Grun. with oval valves (10–25 l.), and *F. virescens* Ralfs are also general; the last belongs to the sect. *Eufragilaria*, whilst the others are included in *Staurosira*. A rarer sp. is *F.* (*Staurosira*) *construens* (Ehrenb.) Grun., with valves showing one or two inflations. *F.* (*Eufragilaria*) *crotonensis* (A. M. Edw.) Kitton (*Nitzschia pecten* Brun.), with elongate valves (40–110 l.) dilated at the middle, is general in the plankton of the Brit. lake areas. The colonies of *Fragilaria* are, according to Schröder, often enveloped in a wide zone of mucilage.

[1] See note, p. 364.

Synedra Ehrenberg, 1831[1]. Frustules linear, much elongated, usually solitary, but sometimes clustered in radiating or fan-shaped colonies which are often epiphytic. Valves commonly needle-shaped, linear or linear-lanceolate, generally with attenuated or subcapitate extremities, mostly straight but occasionally bent or somewhat undulated, finely striated; striae often absent in the middle of the valve, leaving a square or rectangular hyaline area; mucilage-pores frequently present at the ends (fig. 143, C); pseudo-raphe generally evident, often enlarging to a central rounded hyaline space (false nodule (fig. 152, A)) and sometimes with false polar nodules. Girdle-view elongated, with truncate apices. Chromats. two, plate-like, with undulated or indented edges and 2–5 pyrens. Auxosp. (only known in one or two sp.) two from a mother-cell.

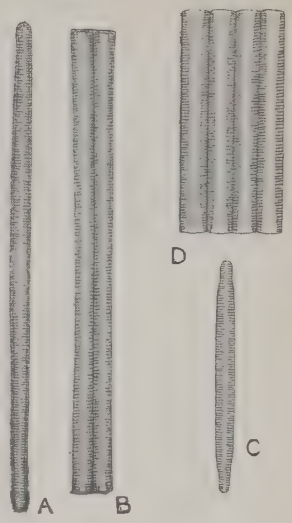

Fig. 152. A and B, *Synedra pulchella* Kütz., from Cambridge (× 500). C and D, *Fragilaria capucina* Desmaz., from Shipley, W. Yorks (× 520).

The sp. of this genus are very variable and no two authorities are in any way in agreement as to their classification. It may be doubted whether Meister[2] is right in utilising the presence or absence of a hyaline area in the middle of the valves as a basis for grouping the sp., since it seems to remove nearly allied forms from one another.

There are about ten Brit. freshw. sp., several of which are common, being found in almost every kind of suitable locality and often occurring in immense abundance in the waters of lakes and springs. The most frequent are: *S. Ulna* (Nitzsch) Ehrenb., with valves (70–400 l.) having somewhat rostrate apices and with the striae usually interrupted in the middle; *S. pulchella* Kütz. (fig. 152, A, B; 60–130 l.), with a false central nodule; and *S. Acus* (Kütz.) Grun., with needle-like valves with slightly capitate apices (100–250 l.). All three are found generally in the plankton of the Brit. lakes. *S. splendens* Kütz. (fig. 143, C) (regarded by some as a var. of *S. Ulna*) has valves (up to 340 l.) arranged in radiating groups attached to other aquatics. *S. capitata* Ehrenb., with markedly enlarged apices, is general, but not so common as the previous sp. Free-floating clusters are

[1] Provazek, Österr. Bot. Zeitschr. L, 1900, p. 69.
[2] Kieselalg. d. Schweiz, p. 69.

characteristic of *S. actinastroides* Lemm., hitherto only once recorded for the Brit. Isles (West, 1911, p. 87).

Asterionella Hassall, 1850[1]. Frustules narrow and linear, joined by delicate mucous cushions at their basal extremities to form stellate colonies. Valves narrowly linear-fusiform, with delicate transv. striae and capitate apices, one apex (the lower) being larger than the other; pseudo-raphe very delicate with an enlargement in each apex. Girdle-view linear, with dilated truncate extremities. Chromats. two, one in front of the other.

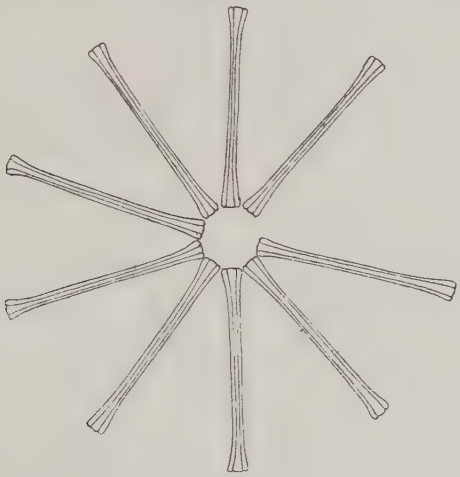

Fig. 153. *Asterionella gracillima* Heib., from the plankton of Lough Neagh, Ireland (×450).

A. gracillima Heib. (fig. 153) and *A. formosa* Hass.[2] are regular and abundant constituents of the Brit. freshwater plankton; the latter is also common in the quiet waters of ditches, ponds, and lakes. Valves 70–100 l., but in *A. gracillima* they may reach 130 μ. In this sp. both ends of the valves are nearly the same, but in *A. formosa* both valve- and girdle-views are distinctly broader at the lower than at the upper ends. The colonies of this genus are somewhat fragile and easily become dismembered. According to Voigt[3], delicate mucilage-films are spread out between the individual frustules.

[1] cf. Bachmann, 1907, p. 70.

[2] In the earlier edition of this work the form depicted in fig. 153 was described as *A. formosa* Hass., but in this species the girdle-view is much broader at the base than at the apex. Schütt (loc. cit. p. 118) likewise confuses the two species.

[3] Biol. Centralbl. xxi, 1901, p. 36.

Family 5. EUNOTIACEAE

The frustules are usually free-floating and either solitary or joined to form ribbons; in a few cases they occur as epiphytic tufts. The more or less curved or arcuate valves are dorsiventral, the dorsal edge being often undulate, the ventral one concave. There is a reduced raphe, or a pseudo-raphe with distinct polar nodules, situated more or less close to the ventral margin. There are no septa. Each frustule contains two parietal, plate-like chromatophores.

Ceratoneis Ehrenberg, 1840. Frustules solitary, or united to form short bands, free-floating. Valves arcuate, with a more or less prominent swelling in the middle of the concave side, and obtuse, subcapitate, or rostrate-capitate apices; transv. striae interrupted by a well-marked pseudo-raphe approximated to the ventral margin; central and, especially, polar nodules distinct. Girdle-view linear, rectangular.

C. Arcus (Ehrenb.) Kütz. (*Eunotia Arcus* W. Sm. (fig. 154, D)) is frequent in mountainous areas, esp. streams; valves with obtuse apices, 35–100 l. The var. *Amphioxys* (Rabenh.) De Toni, distinguished by its produced and subcapitate apices, is abundant in the same localities, and pure gatherings of it are by no means uncommon; valves up to 85 l.

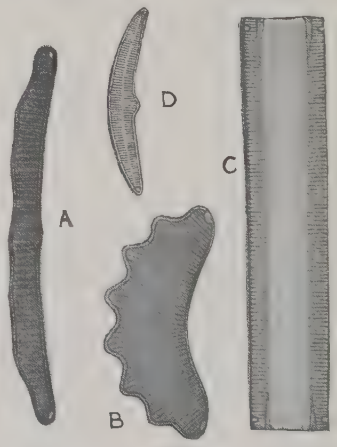

Fig. 154. A, *Eunotia pectinalis* (Kütz.) Rabenh. var. *undulata* Ralfs, from Baildon, W. Yorks (×600). B, *E. robusta* Ralfs, from Dolgelly, Wales (×600). C, *E. gracilis* (Ehrenb.) Rabenh., from Lerwick, Shetlands (×500). D, *Ceratoneis Arcus* Kütz., from Cautley Spout, W. Yorks (×520).

Eunotia Ehrenberg, 1837[1] (*Himantidium* of various authors; *Desmagonium* Ehrenberg, 1848; *Climacidium* Ehrenberg, 1867). Frustules rectangular, either (*a*) united by their valve-faces to form long flexuose, ribbon-like filaments (sect. *Himantidium*) or (*b*) solitary, more rarely as epiphytic clusters on other Algae (sect. *Eunotia*). Valves arcuate or bow-shaped, the dorsal margin often undulate or nodulose, apices mostly produced, obtuse or more often

[1] Hustedt, Abh. Nat. Ver. Bremen, xx, 1911, pp. 99, 274.

subcapitate, with uninterrupted transv. striae composed of fine dots; pseudo-raphe situated along the ventral margin, inconspicuous; no central nodule, polar nodules elongate, comma-shaped, evident (also in girdle-view) or indistinct. Girdle-view rectangular, transv. striated at the margin. Chromats. two, apposed to the two valves, their lobes spreading on to the ventral girdle (fig. 157, F). Auxosp. formed by conjug. of protoplasts of two mother-cells.

There are about ten Brit. sp. In the sect. *Himantidium* the two most frequent are *E. gracilis* (Ehrenb.) Rabenh. (figs. 154, C; 157, F), in which the narrow valves have capitate apices, and *E. pectinalis* (Kütz.) Rabenh., with numerous vars. (cf. fig. 154, A). In the other sect. *E. lunaris* (Ehrenb.) Grun. is much the commonest; the narrowly linear arcuate valves (50–90 l.) generally occur in tufts attached by a small mucilage-cushion to other aquatics. *E. tetraodon* Ehrenb., *E. incisa* Greg., and *E. bicapitata* Grun. (*Synedra biceps* W. Sm.; *E. flexuosa* var. *bicapitata* Grun.) are general in mountainous areas.

Series II. ACHNANTHOIDEAE

Family ACHNANTHACEAE

The outstanding characteristics of this family of epiphytes are (*a*) the possession of two dissimilar valves, the one having only a pseudo-raphe, the other a true raphe and nodules, and (*b*) the curved or bent girdle-view. The valves are straight and either isobilateral or clavate. Longitudinal septa occur in *Rhoicosphenia*, but not in the two other genera. There is usually a single parietal chromatophore. The auxospores are formed in various ways.

Achnanthes Bory, 1822 (*Achnanthidium* Kützing, 1844; Grunow, 1880; *Microneis* Cleve, 1895). Frustules straight and symmetrical in valve-view, but geniculate and asymmetrical in girdle-view, being bent along the transv. axis, either free-floating and solitary, or as single frustules or short rows of frustules epiphytic by means of a short or long mucilage-stalk on other aquatics. Valves linear or fusiform, often with capitate apices; one valve convex with a pseudo-raphe without any trace of nodules, the other concave with a true raphe and both central and polar nodules and sometimes a distinct stauros (cf. fig. 155, A–C); valves with transv. striae consisting of rows of fine or coarse punctae, sometimes with intervening costae, markings usually slightly different on the two valves. Chromats. mostly one thick parietal plate lying against the convex valve, less

often numerous small granules. Auxosp. formed either by conjug. or from the products of division of single parent-cells (cf. pp. 346, 347).

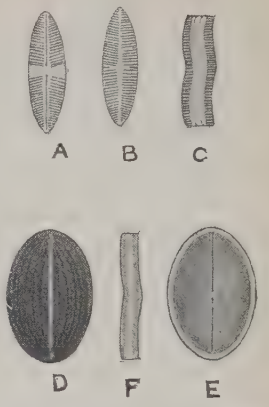

Fig. 155. A–C, *Achnanthes Hungarica* Grun., from near Sutton, Cambridge (× 520). D–F, *Cocconeis Placentula* Ehrenb., from Sheep's Green, Cambridge (× 520).

There are two principal sections, viz. *Euachnanthes* Schütt in which raphe and pseudo-raphe are straight and median or a little excentric, and *Achnanthidium* Kütz. in which raphe and pseudo-raphe are sigmoid. Cleve's *Microneis* includes those sp. of the former in which the striae are composed of minute punctae, and the same author has distinguished a number of other subgenera[1]. Of the nine Brit. sp. one of the largest, though rather rare, is *A. coarctata* Bréb.; the valves (18–43 l.) have a slightly curved raphe. *A. exilis* Kütz., *A. linearis* W. Sm., and *A. microcephala* Kütz. are very small sp. which are often abundant as stalked epiphytes on filamentous Algae; all three have finely punctate striae and the last is characterised by slightly capitate valves. *A.* (*Achnanthidium*) *flexella* (Kütz.) Bréb. possesses a sigmoid raphe and often occurs in quantity in hilly districts; valves 35–50 l.[2] The marine *A. brevipes* Ag. has been recorded from the canal at Droitwich, Worcestershire.

Cocconeis Ehrenberg, 1835[3] (*Orthoneis* Grunow, 1868; *Eucocconeis* Cleve, 1895). Frustules flat and plate-like (somewhat the shape of a concavo-convex lens), symmetrical in the valve-view, but bent or arched in the girdle-view, epiphytic, attached by their lower valve-faces to diverse aquatics. Valves broadly elliptical or subcircular; the upper valve convex with a pseudo-raphe (fig. 155, D), the lower concave with a raphe and central nodule, though polar nodules are generally indistinct (fig. 155, E); valves with punctate striae, transv. in the middle and radiating towards the poles, and sometimes with marginal costae representing a system of narrow marginal transv. septa. One parietal chromat. with a lobed margin, mostly lying against the convex valve. Auxosp. formed by conjug. of two cells, or a single auxosp. formed from one mother-cell.

There are many marine sp. of this genus, but only two —*C. Pediculus* Ehrenb. and *C. Placentula* Ehrenb. (fig. 155, D–F)—inhabit freshwater, both of them being abundant epiphytes on filamentous Algae and other

[1] Cleve, loc. cit. 1895, p. 187.
[2] This sp. is placed by Cleve (p. 179) in a section *Eucocconeis* of *Cocconeis*.
[3] Karsten, Flora, LXXXVII, 1900, p. 253.

aquatics all over the Brit. Isles; *Cladophora* and *Vaucheria* are often completely covered by their frustules. *C. Pediculus* is distinguished from the other sp. by its rhombic-elliptic valves, the lower valve lacking the hyaline intramarginal zone of *C. Placentula*. Both have valves 12–35 l.

Rhoicosphenia Grunow, 1860. Frustules in girdle-view wedge-shaped, considerably curved, attached by mucous cushions or stalks to other aquatics. Valves clavate, one pole larger than the other, with punctate striae; upper valve possessing only a pseudo-raphe and no nodules, the lower with a raphe and central and polar nodules. Longit. septa two, each with a very large foramen, appearing as short ribs in the girdle-view. Chromat. one, parietal, apposed to one of the girdles.

This genus has often been classed with the Gomphonemaceae, with which valve- and girdle-views show much resemblance. *R. curvata* (Kütz.) Grun. (fig. 161, H) is common all over Britain, often clothing in dense masses the thicker branches of sp. of *Cladophora*; valves 13–45 l.

Series III. NAVICULOIDEAE

Family 1. NAVICULACEAE

The Diatoms of this family are exceedingly numerous and well-defined. The frustules are generally straight and symmetrical in three planes at right angles (*Navicula*, *Stauroneis*), or they may be sigmoid (*Gyrosigma*), or twisted (*Amphiprora*). The raphe is mostly median, with well-marked central and polar nodules, and there is a system of striae or costae on either side of it; in *Stauroneis* the central nodule forms a wide stauros (fig. 156, E, F), and in the various subgenera of *Navicula* it and the raphe show diverse accessory developments. There are generally two large parietal plate-like chromatophores (fig. 157, D, E), mostly without pyrenoids, principally disposed over the girdles but often extending on to the valve-faces; sometimes the two are connected by a median bridge. Auxospores are formed either in pairs by conjugation of two individuals following a fission of each protoplast (fig. 145, A), or singly by rejuvenescence of the contents of a single cell (fig. 145, C, D).

The frustules are mostly solitary and free-floating, but in some forms they are enclosed in a tough tubular mucilage-envelope which is often much branched; some of the marine forms are attached to a substratum by hyaline stalks.

Navicula Bory, 1822 (*Pinnularia* Ehrenberg, 1843; *Schizonema* Agardh, 1824; *Colletonema* de Brébisson, 1849; *Diadesmis* Kützing, 1844). Frustules usually solitary and free-floating,

more rarely enclosed in mucous tubes, some sp. terrestrial. Valves quite straight and symmetrical with regard to the line of the raphe, of very variable form though predominantly lanceolate or fusiform; valves with striae or costae of variable strength, often composed of rows of punctae, more or less transv. or sometimes somewhat radiating, never quite reaching up to the usually straight raphe, and commonly shorter or almost interrupted opposite the central nodule; in rare cases there is a smooth longit. area of some width on each side of the raphe. Girdle-view straight, rectangular.

Navicula is much the largest genus of Diatoms, embracing upwards of 1000 species, which occur widely distributed in fresh, brackish, and salt water, as well as in the soil; many fossil forms are also known. Cleve (loc. cit. 1894, p. 10) classes a large number of the sp. in separate genera (*Diploneis*, *Neidium*, *Caloneis*, etc.) equivalent to *Stauroneis*, *Amphipleura*, etc., and this procedure has been followed by some authorities, whilst others regard some or all of them merely as subgenera. The more important of these, as far as freshwater and terrestrial forms are concerned, are as follows:

Diploneis Ehrenberg, 1840: central nodule more or less square, prolonged at either end into pairs of horn-like processes enclosing the raphe; on either side of these processes lies a longit. furrow parallel to the line of the raphe; two chromats., e.g. *N. ovalis* Hilse, *N. elliptica* Kütz. (fig. 161, C).

Caloneis Cleve, 1894: valves with delicate non-punctate striae which are traversed by one or more longit. lines running parallel to the margin of the valve; two chromats., e.g. *N. Amphisbaena* Bory (fig. 145, C).

Neidium Pfitzer, 1871: valves with parallel punctate striae, running obliquely to the longit. axis and traversed by one or two longit. lines; four chromats., e.g. *N. Iridis* Ehrenb. (fig. 161, B).

Anomoeoneis Pfitzer, 1871: valves with transv. striae composed of fine dots or striulations which are arranged in wavy or oblique longit. lines: a single lobed chromat., with a median pyren., apposed to one girdle and overlapping on to the valves, e.g. *N. sphaerophora* Kütz. (fig. 156, C), *N. serians* (Bréb.) Kütz. (fig. 156, D).

Frustulia Agardh, 1824 (*Vanheurckia* Brébisson, 1868): valves with elongated polar and central nodules enclosed, along with the raphe, between two parallel siliceous ribs; frustules occasionally in a linear series within a mucous tube; two chromats.[1], e.g. *N. rhomboides* Ehrenb. (fig. 157, A, B).

Pinnularia Ehrenberg, 1843: many large forms; valves with relatively coarse transv. costae not composed of punctae and in some

[1] According to West (1904, p. 294) this is the *Frustulia* as amended by Rabenhorst in 1851, but not that of Agardh.

cases traversed by two longit. lines (cf. p. 340); two chromats. with pyrens. e.g. *N. alpina* (W. Sm.) Ralfs (fig. 156, A).

The sp. remaining in *Navicula* proper are very numerous and are grouped by Cleve in a number of sections based on the markings of the valves; the striae are mostly punctate, but in *N. cryptocephala* Kütz., etc. they are composed of small fine lines (*Naviculae lineolatae*), whilst in a few cases they are quite structureless.

As in other of the big Diatom genera, whilst there are many easily characterised sp., a large number are insufficiently described or probably merely habitat-forms of others. About 80 freshwater and terrestrial sp. are known to occur in the Brit. Islands, the aquatic

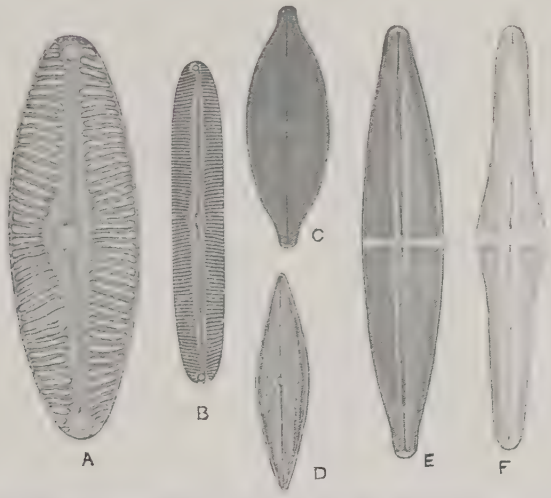

Fig. 156. A, *Navicula alpina* (W. Sm.) Ralfs, from Lerwick, Shetlands (×400). B, *N. viridis* Kütz., from Baildon, W. Yorks (×400). C, *N. sphaerophora* Kütz., from Wimpole Park, Cambridge (×500). D, *N. serians* (Bréb.) Kütz., from Mickle Fell, N. Yorks (×400). E, *Stauroneis Phoenicenteron* (Nitzsch) Ehrenb., from Adel Bog, W. Yorks (×400). F, *S. acuta* W. Sm., from Shipley Glen, W. Yorks (×450).

forms favouring stagnant water. The most striking are *N. cuspidata* Kütz., *N. nobilis* Ehrenb. (fig. 142), *N. major* Kütz., *N. alpina* Ralfs (fig. 156, A), and *N. lata* Bréb., all except the first belonging to the subgenus *Pinnularia*; the two last-mentioned sp. prefer boggy tracts in elevated regions, in which localities they are sometimes frequent. *N. perpusilla* Grun. is one of the smallest Brit. sp. (12·5 l.), whilst *N. nobilis* Ehrenb. is the largest (200–400 l.). One of the commonest is *N.* (*Pinnularia*) *viridis* Kütz. (figs. 156, B and 157, D and E). There are two Brit. sp. belonging to the subgenus *Frustulia*, viz. *N. rhomboides* Ehrenb. (fig. 157, A, B) and *N. vulgaris* Thw. A variety of the former—var. *saxonica* Cl. (*N. crassinervia* Bréb.)—is very abundant

and widely distributed in the Brit. Isles, being very frequent in boggy districts; valves 50–80 l. Pure gatherings of it can often be collected from *Sphagnum*-pools. *N.* (*Pinnularia*) *borealis* Ehrenb., *N. mutica* Kütz. (fig. 161, D), and *N. atomus* Naeg. are widely distributed in cultivated soils.

Some of the small and abundant sp., such as *N. exilis* Kütz., are remarkable for the rapidity of their movements.

Stauroneis Ehrenberg, 1843 (*Pleurostauron* Rabenhorst, 1859; *Schizostauron* Grunow, 1867). Frustules solitary and free-floating (sect. *Stauroneis*) or attached by their valve-faces to form short filaments (*Pleurostauron*). Essential difference from *Navicula* is the transv. dilation of the central nodule to form a stauros over which the striae are lacking; striae radiating, finely punctate. In the sp. grouped by Rabenhorst in *Pleurostauron* there are short diaphragms (longit. septa) extending a little way from the apex of the frustule inwards; these appear as folds in the girdle-view and are very evident in the valve-view (fig. 156, F). Auxosp. formed singly by conjug. of two individuals.

There are about six Brit. freshwater sp., of which *S. Phoenicenteron* Ehrenb. (fig. 156, E) is the largest (100 170 l.) and most frequent. *S.* (*Pleurostauron*) *acuta* W. Sm. (fig. 156, F) is local, being usually found in bogs.

Amphipleura Kützing, 1844. Frustules solitary, free-floating. Valves narrowly lanceolate with acute rounded apices and, often exceedingly fine, transv. and longit. striae composed of minute

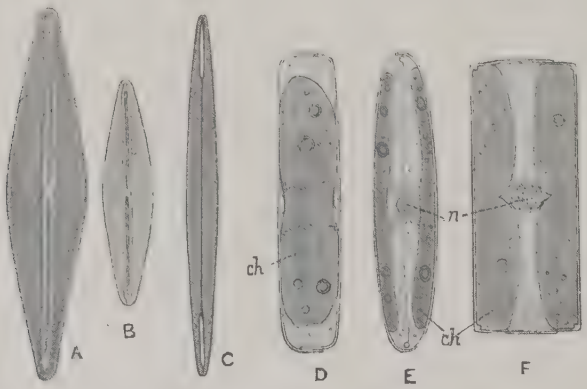

Fig. 157. A and B, *Navicula* (*Frustulia*) *rhomboides* Ehrenb., from Mickle Fell, N. Yorks (×520). C, *Amphipleura pellucida* Kütz., from Chippenham Fen, Cambridge (×520). D and E, girdle- and valve-views of *Navicula viridis* Kütz., and F, *Eunotia gracilis* (Ehrenb.) Rabenh., girdle-view, to show chromatophores (*ch* and nucleus (*n*), ×400.

punctae; central nodule greatly elongated, appearing as a narrow rib separating the two short distal portions of the raphe, which are enclosed between two parallel ribs uniting at each extremity of the valve to form the polar nodules. Two auxosp. formed by conjug. of two individuals.

Only one sp., *A. pellucida* Kütz. (fig. 157, C), inhabits Brit. freshwaters, but it is generally distributed and often abundant; valves 80–140 l. Some very large forms sometimes occur in the plankton. The striae are exceedingly fine (about 37 in 10 μ) and the valves are used as microscopic test-objects.

Gyrosigma Hassall, 1845 (*Pleurosigma* W. Smith, 1853). Frustules solitary, free-floating, generally straight and linear-oblong in the girdle-view. Valves convex, sigmoid, with obtuse or attenuated extremities, provided with two sets of striations which cross one another either at right angles or obliquely; median line very narrow, central nodule small; raphe sigmoid. Chromats. two (sometimes four) large, entire or jagged, perforated plates, disposed in the manner common to all Naviculaceae, with pyrens.; in some of the marine forms there are numerous band-shaped or discoid chromats.

There are only four Brit. freshwater sp., of which *G. attenuatum* (Kütz.) Rabenh. (fig. 158, A; valves 190–250 l.) and *G. Spencerii* (Queck.) O. K. (valves 80–130 l.) are the most abundant; in the former the longit. striae are further apart than the transv. ones, whilst in the latter the converse obtains. In *G. acuminatum* Kütz. the two sets are equally spaced.

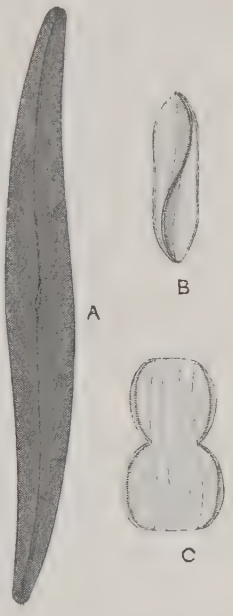

Fig. 158. A, *Gyrosigma attenuatum* (Kütz.) Rabenh., from Chippenham Fen, Cambridge (×400). B and C, *Amphiprora paludosa* W. Sm., from Wimbledon Common, Surrey (×400).

Amphiprora Ehrenberg, 1843; emend. Cleve, 1891 (*Amphicampa* Rabenhorst, 1864). Frustules free-floating, solitary, with a slight twist around the longit. axis. Valves convex, naviculoid in form, with cuneate apices and fine transv. striae, with a prominent sigmoid keel in which is situated the sigmoid raphe (fig. 158, B); central and polar nodules small; valves with two delicate curved lines, extending from the keel to the apices.

Girdle-view broadly inflated, with a median constriction and truncate ends, showing longit. sutures due to intercalary bands; girdle itself slightly twisted. Seen obliquely, the sigmoid keels of the two valves cause the frustules to appear much more twisted than is truly the case. Chromats. one or two large plates.

Of the two Brit. freshwater sp., *A. paludosa* W. Sm. (fig. 158, B and C) is often found, and sometimes in abundance, in small ponds and ditches; valves 40 80 l. *A. ornata* Bailey, in which the longit. sutures are undulate, is much rarer.

Mastogloia Thwaites, 1848. Frustules naviculoid, commonly embedded in a gelatinous envelope of considerable size. Valves usually elliptic-lanceolate, generally with produced extremities, with transv. striations radiating somewhat in the centre; raphe straight, median, with central and polar nodules. Longit. septa two, perforated by a large oval foramen, the marginal part of the valve divided, except at the ends of the frustule, into a row of radially arranged chambers; the septa between these chambers appear as ribs (absent at the ends) in the valve-view and as two longit. series of broad marks in the girdle-view. Chromats. two or four, usually apposed to the valves. Two auxosp. formed by conjug. of two individuals.

Fig. 159. *Mastogloia Smithii* Thw., from Baildon, W. Yorks (×500). *A*, valve-; *B*, girdle-view.

Of the four Brit. freshwater sp., *M. Smithii* Thw. (fig. 159; valves 30-45 l.) and *M. Dansei* Thw. are the most generally distributed; in the latter the valves have cuneate extremities.

Family 2. GOMPHONEMACEAE

Since the removal of *Rhoicosphenia* to the Achnanthaceae, this includes only the genus

Gomphonema Agardh, 1824. Frustules wedge-shaped, straight, generally attached by their inferior (smaller) extremities to a more or less branched system of hyaline mucilage-stalks arising from some substratum. Valves usually with one end conspicuously larger than the other, often lanceolate or clavate, or sinuate at the margins, mostly with well-marked more or less radiating striae, sometimes consisting of distinct beads and visible also at the edges of the girdle-view; axial area wide or narrow, striae often shorter opposite the central nodule, here in some sp. are found one or several isolated unilateral punctae (*Stigmaticae* Cleve (cf. fig. 1, F)); raphe straight, median, with well-marked central and polar nodules. Girdle-view cuneate. Chromat. one,

large, parietal, somewhat sinuate, apposed to one of the girdles, but extending over on to the valve-faces and most of the other girdle. Two auxosp., lying parallel to one another, are formed from two mother-cells without conjug.

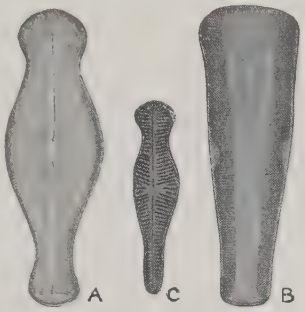

Fig. 160. A and B, *Gomphonema geminatum* (Lyngb.) Ag., from Cautley Spout, W. Yorks (×400). C, *G. constrictum* Ehrenb., from Chippenham Fen, Cambridge (×400).

There are about 14 Brit. freshwater sp., some of which, such as *G. constrictum* Ehrenb. (fig. 160, C), *G. acuminatum* Ehrenb. (fig. 1, F), and *G. parvulum* Kütz., are common in every part of the Brit. Isles, being frequent epiphytes on other Algae. *G. geminatum* (Lyngb.) Ag., the largest sp. with valves 90–120 l. and a maximum breadth of 35–40 (fig. 160, A, B), is principally confined to hilly districts, often forming thick felt-like masses of a greyish-white colour on dripping rocks.

Family 3. CYMBELLACEAE

The members of this family probably do not form a natural group, their chief characteristic being the bent or sublunate form of the valves, while the girdle-view is straight and often subrectangular or elliptic; the frustules are thus symmetrical about a longitudinal plane parallel to the valve-faces and a median transverse plane at right angles to the valves. The latter are commonly more or less prominently crested or keeled, and the ventral girdle is often narrower than the dorsal one (cf. p. 338), so that the general form of the cross-section is trapezoidal. The raphe is usually curved and not median, being nearer to one edge of the valve. There is mostly one large, lobed, parietal chromatophore with a pyrenoid, the median part of which is disposed within the convex girdle-face, but in several species of *Amphora* there are two or several chromats. For auxospores, see the genera.

Cymbella Agardh, 1830 (*Cocconema* Ehrenberg, 1829; *Encyonema* Kützing, 1833). Frustules more or less of the form of the segments of an orange, dorsiventral, straight or more usually sublunate, free, or on gelatinous stalks and epiphytic, or enclosed in gelatinous tubes (*Encyonema*). Valves strongly attenuated from the middle towards the obtuse extremities, dorsal margin strongly convex, ventral margin slightly convex or concave and in the latter case generally tumid in the middle;

valves with slightly radiating striae, often composed of distinct series of dots, more closely placed on the ventral than on the

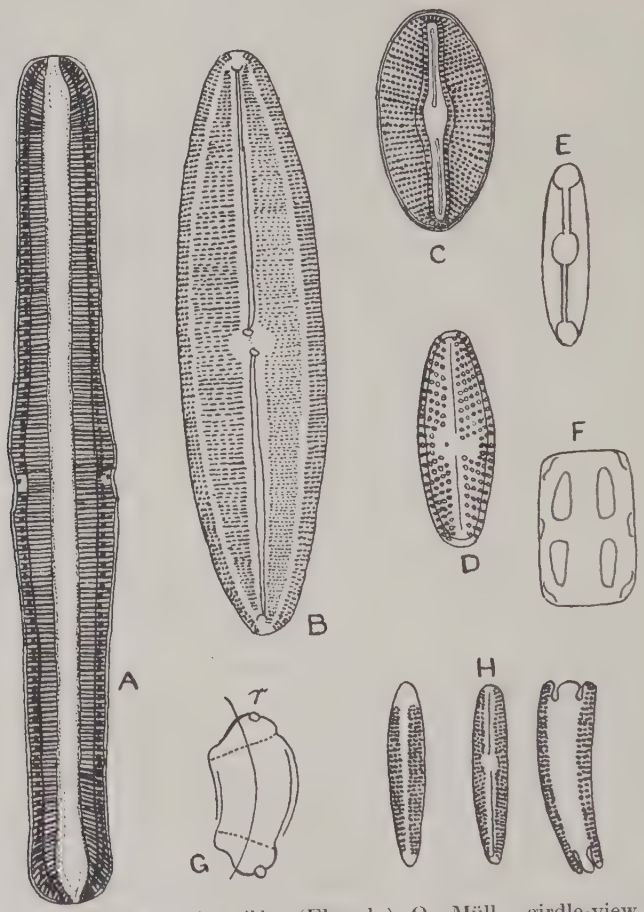

Fig. 161. A, *Rhopalodia gibba* (Ehrenb.) O. Müll., girdle-view (after Meister, ×600). B, *Navicula* (*Neidium*) *Iridis* Ehrenb., valve (after Meister, ×600). C, *Navicula* (*Diploneis*) *elliptica* Kütz., valve (after Meister, ×600). D, *N. mutica* Kütz., forma (after Bristol, ×1435). E, valve- and F, girdle-view of *Diatomella Balfouriana* Grev. (after Carter, ×1420). G, *Rhopalodia gibberula* (Ehrenb.) Müll., section of frustule (after Müller); *r*, raphe. H, *Rhoicosphenia curvata* Grun. (after Meister, ×600), showing respectively the upper (left) and lower valves, and the girdle (on the right).

dorsal side, isolated dots adjacent to the central nodule in some sp.; raphe well-marked, straight or more commonly curved, nearer the ventral margin of the valve, terminal fissures straight

or curved towards the dorsal margin. Girdle-view straight, often subrectangular, one girdle narrower than the other (cf. fig. 143, F). Auxosp. formed in pairs, either by conjug. of the divided protoplasts of two individuals or, without conjug., by rejuvenescence of the contents of two parent-cells (West, 1916 *a*, p. 108).

There are some 15 Brit. sp. *C. lanceolata* Ehrenb. is the largest (80–150 l.) and one of the most abundant (fig. 162, A). *C. Cistula* Hemp. and *C. cymbiformis* Ehrenb. are smaller sublunate sp. which are almost equally frequent. *C. cuspidata* Kütz., with unequally biconvex valves, is widely distributed and often abundant on wet rocks in mountainous regions, frequently forming gelatinous masses of a greyish-brown colour. The frustules of *C. prostrata* Berk., *C. caespitosa* Kütz., and *C. gracilis* Rabenh. occur in more or less linear series within gelatinous tubes.

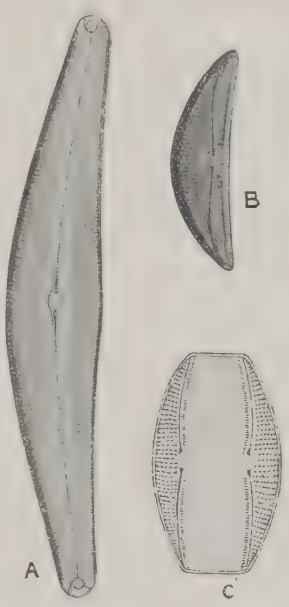

Fig. 162. A, *Cymbella lanceolata* Ehrenb., from Shipley Glen, W. Yorks (×500). B and C, *Amphora ovalis* Kütz., from Moidart, Inverness (×500).

Amphora Ehrenberg, 1831. Frustules solitary, generally free-floating, elliptical with truncate apices in the girdle-view; girdle often with irregular longit. striations, the dorsal one wider than the ventral one. Valves curved or sublunate, with a more or less median crest (resembling a gable in cross-section (cf. fig. 143, G)), the curved raphe close to the ventral (concave) surface (fig. 143, H); striation of valves similar to that of *Cymbella*. Chromats. very variable, one, two, or four large plates in diverse positions, or a large number of granules arranged in the form of a network[1]. Auxosp. formed in pairs by conjug. of the divided protoplasts of two individuals.

Since the valves in this genus are markedly arched, with two sloping faces forming an acute or obtuse angle, an actual valve-view is never obtained and disconnected valves present either the dorsal or the ventral face to the observer; for the same reason the intact frustules are always seen in girdle-view, in which, however, one of the two faces of each valve is also more or less

[1] Mereschkowsky, Script. Bot. Hort. Univ. Imp. Petropolitani, XXI, 1903, p. 145.

completely shown (fig. 162, C). The raphe is situated near the lower margin of the ventral valve-face.

Most of the sp. are marine, but three Brit. freshwater sp. are known, of which *A. ovalis* Kütz. (fig. 162, B, C) is common; valves 50–70 l. A very small variety of it—var. *pediculus* Kütz.—occurs as an epiphyte, generally on other Diatoms, e.g. *Nitzschia sigmoidea*.

Epithemia de Brébisson, 1838[1]. Frustules solitary, attached by their ventral (concave or plane) surfaces to other aquatics, subrectangular or broadly elliptical with truncate apices in the girdle-view. Valves slightly curved or lunate, the ventral margin concave or almost straight, with strong transv. ribs between which are conspicuous rows of punctae; raphe (or pseudo-raphe in some sp.?) typically V-shaped, the central nodule being in the middle, or nearer the dorsal margin, of the valve and the two branches of the raphe curving rapidly towards the ventral margin which they follow for the greater part of their course (fig. 163, B). Ribs on the valves corresponding to transv. septa which are apparent also in the girdle-view (fig. 163, C, D); in some sp. there are two longit. septa (fig. 143, B) perforated by a row of rounded foramina[2] which open into the chambers between the transv. septa, the inner ends of which then terminate in small globular expansions (fig. 163, D). Chromats. one or two large plates. Auxosp. in pairs, formed as in *Amphora*.

The genus is almost entirely confined to fresh or brackish water and five Brit. sp. are known. *E. turgida* (Ehrenb.) Kütz. (valves 70–150 l.) (fig. 163, B, C) is the most abundant, but *E. zebra* (Ehrenb.) Kütz., with 3–5 rows of punctae between each pair of ribs, is also common in all kinds of localities. *E. Argus* (Ehrenb.) Kütz. var. *alpestris* (W. Sm.) Rabenh. often occurs in large quantities in mountainous areas; *E. Argus* is one of the sp. possessing longit. septa (fig. 163, D).

Rhopalodia O. Müller, 1895[3]. Frustules solitary and free-floating, usually presenting the girdle-view which is elliptic to linear or club- to pear-shaped, with a prominent constriction in the often somewhat inflated middle region (fig. 161, A); one girdle slightly wider than the other (fig. 161, G). Valves prominently keeled, in outline either (*a*) elongate and straight with incurved apices, sometimes prominently arched in the middle of the dorsal margin, or more rarely (*b*) comma-shaped with unequal poles; valves with well-marked transv. ribs and intervening delicate striae; raphe situated in the keel (apparently on the dorsal

[1] Müller, Ber. Deutsch. Bot. Ges. IV, 1886, p. 308.

[2] The partitions between these foramina are usually broken near the ventral margin (e.g. in *E. Argus*).

[3] Engler Bot. Jahrb. XXII, 1895, p. 54; Hedwigia, XXXVIII, 1899, p. 286.

margin), occupying the extreme edge of the frustule in the girdle-view; central and polar nodules often evident. A transv. septum developed at either end of the valve. Auxosp. as in *Epithemia*.

The valves in this genus have much the same crested character as those of *Amphora* and, as in that genus, the intact frustules are nearly always seen in the girdle-view, which is bounded by the adjacent parts of the valve-faces.

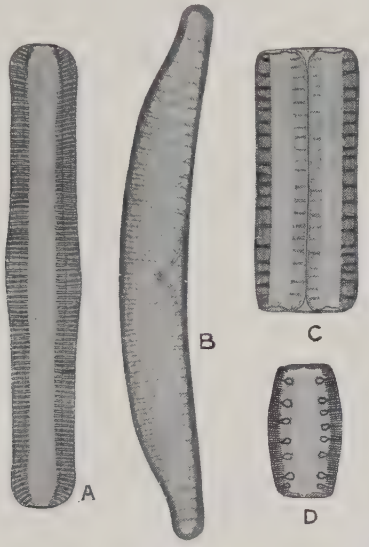

Fig. 163. A, girdle-view of *Rhopalodia gibba* (Ehrenb.) Müll., from Wicken Fen, Cambridge. B, valve-view of *Epithemia turgida* (Ehrenb.) Kütz., from Keighley, W. Yorks. C, girdle-view of dividing specimen of *E. turgida*, from Lerwick, Shetlands. D, girdle-view of *E. Argus* (Ehrenb.) Kütz., from Wicken Fen, Cambridge. (All × 450.)

All the sp. occur in freshwater and two are recorded for the Brit. Isles. *R. gibba* (Ehrenb.) O. Müll. (*Epithemia gibba* Kütz.) is common in all kinds of localities (figs. 161, A; 163, A); the smaller *R. gibberula* (Kütz.) Müll. (*E. gibberula* Kütz.) is rarer, but its var. *producta* Grun. is often abundant in mountainous regions. In both sp. the valves are straight, with incurved apices.

Series IV. NITZSCHIOIDEAE

Family NITZSCHIACEAE

The members of this family are sharply characterised by the keeled valves and the rhombic transverse section of the frustules (fig. 164, D). The keel shows conspicuous carinal dots, which

represent the partitions between narrow canals by which the raphe communicates with the interior of the cell. The frustules are elongated and usually asymmetrical, not uncommonly showing a more or less sigmoid curvature in the girdle-view, though the valve-view is generally straight. The simple canal-like raphe is situated in the keel (cf. p. 338). The chromatophore is either a diagonal plate (sometimes two), or there are one or two curved parietal plates, the median portions of which are apposed to the girdles; pyrenoids numerous and small.

Bacillaria Gmelin, 1788. Frustules straight, forming plate- or ribbon-like colonies which exhibit a characteristic gliding movement of one frustule over another. Girdle-view linear with truncate apices and a row of carinal dots along each lateral margin. Valves slightly convex, narrowly linear in outline, transv. striated, with attenuated apices and a median keel containing the raphe and provided with a row of rounded carinal dots.

B. paradoxa Gmel. (fig. 164, I), the only Brit. sp., occurs in the freshwater dykes and drains of the north-east and east of England and is also known from the Midlands and the Thames; valves 60–70 l.

Nitzschia Hassall, 1845; emend. Grunow, 1880[1] (*Tryblionella* W. Smith, 1853; *Nitzschiella* Rabenhorst, 1864). Frustules solitary and free-floating, rarely enclosed in mucilage-tubes (*Homoeocladia* Agardh), a few sp. terrestr. Girdle-view often elongate, with parallel margins and truncate apices, either sigmoid or straight, sometimes with inflated sides or a median constriction. Valves elongate, linear or elliptic-lanceolate, straight or more rarely curved, with attenuated and capitate or even rostrate apices, provided with delicate and closely placed transv. striations; keel (with the raphe) more or less marginal, the keels of the two valves being diagonally opposite, so that they occur on different girdle-faces; carinal dots rounded or prolonged into short ribs, the middle ones often a little further apart, less numerous than the striae. Chromats. usually two large plates apposed to the girdles.

The numerous sp., many of which are marine, are largely distinguished by the form of the girdle- and valve-views and the shape and density of arrangement of the carinal dots. There are about 24 Brit. freshwater sp., of which *N. palea* Kütz., with straight valves with attenuated apices (fig. 164, F; 20–65 l.), and *N. sigmoidea* (Ehrenb.) W. Sm., with slightly sigmoid frustules (up to 480 l.), are the most abundant and at the same time exhibit the greatest extremes of size. *N. linearis* (Ag.) W. Sm., with hook-like apices to the valves (fig. 164,

[1] Grunow, K. Svensk. Vet.-Ak. Handl. XVII, 1880, No. 2, p. 67; Mereschkowsky, loc. cit. p. 157.

H), and *N. communis* Rabenh. are common sp. In *N. dubia* W. Sm. the valves (90–160 l.) are slightly narrowed in the middle and have broad carinal dots. *N. acicularis* W. Sm., a small sp. with greatly produced needle-like extremities to the valves (fig. 164, G), is

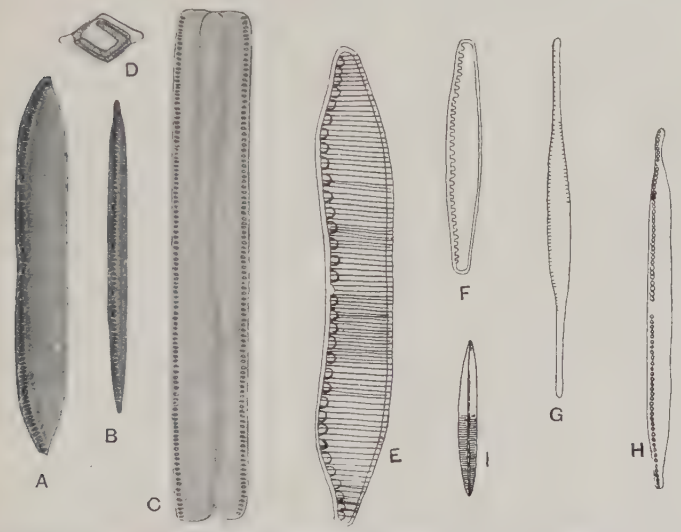

Fig. 164. A and B, two single valves of *Nitzschia dubia* W. Sm., from Hawksworth, W. Yorks (×500). C and D, *N. sigmoidea* (Ehrenb.) W. Sm.; C, short straight, abnormal form in process of division (girdle-view ×400); D, transverse section (after Schütt, from Pfitzer). E, *Hantzschia amphioxys* (Ehrenb.) Grun. (after Bristol, ×1080). F, *N. palea* (Kütz.) W. Sm. (after Bristol, ×1080). G, *N. acicularis* W. Sm. (after Cleve and Grunow). H, *N. linearis* W. Sm. (after Meister, ×600). I, *Bacillaria paradoxa* Gmel.; valve (after v. Schönfeldt).

often exceedingly abundant in ponds and ditches, and is remarkable for the rapidity of its movements. *N. inconspicua* Grun. is fairly frequent in cultivated soils.

Hantzschia Grunow, 1877. Frustules solitary, free-floating or terrestr. Valves somewhat curved with rostrate apices; keel on the concave margin, with very conspicuous carinal dots, the keels of the two valves displaced to the same side of the frustule, so that they lie on the same girdle-face. Girdle-view rectangular. Otherwise like *Nitzschia*.

H. Amphioxys (Ehrenb.) Grun. (fig. 164, E) is the only Brit. freshwater sp.; it is frequently met with and often occurs in prodigious quantity on damp earth, whilst small forms are regularly found in most soils.

Series V. SURIRELLOIDEAE

Family SURIRELLACEAE

In this family the valves are generally strongly costate and symmetrical with regard to a median (often indistinct) pseudo-raphe, whilst the margins are produced into more or less conspicuous wings, the outer edge of which is occupied by a simple canal-like raphe (two to each valve (cf. fig. 144, C and p. 339)). The frustules are always solitary and free-floating and the valves are of very diverse shapes. There are two large much-lobed chromatophores in each cell, one apposed to each valve-face and with lobes projecting into the chambers of the marginal wings (fig. 144, C); in some cases the two chromatophores are connected by a transverse bridge. One auxospore is produced by the conjugation of two individuals.

Cymatopleura W. Smith, 1851. Valve-view broadly elliptical or sublinear, often broadly concave along each margin, with subacuminate apices, the faces of the valves transv. undulate and with very fine transv. striations interrupted by an inconspicuous pseudo-raphe; along the keeled margins are short costae, sometimes simulating coarse beads. Girdle-view (fig. 165, B) linear, with a number of large undulations (corresponding to those on the valve-faces) along the lateral margins. One chromat. apposed to each valve.

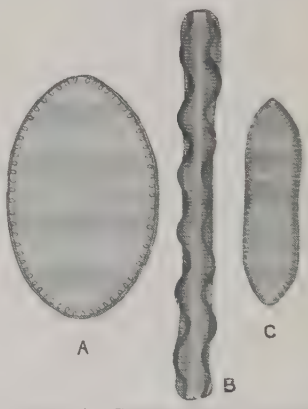

Fig. 165. A, *Cymatopleura elliptica* (Bréb.) W. Sm., from Comberton, Cambridge (×350). B and C, *C. Solea* (Bréb.) W. Sm.; B, girdle-view of large specimen from Esholt, W. Yorks; C, valve-view of small specimen from Cornwall (×350).

There are two Brit. sp., of which *C. Solea* (Bréb.) W. Sm., with elongate valves (50–150 l.) slightly narrowed in the middle, is the commonest (fig. 165, B, C). *C. elliptica* (Bréb.) W. Sm., with broadly elliptical or elliptic-lanceolate valves (80–140 l.), is almost equally abundant (fig. 165, A).

Surirella Turpin, 1827[1]. (Original spelling—"*Suriraya.*") Valve-view elliptical, linear, ovate, or rarely twisted; valve-

[1] Karsten, Flora, LXXXVII, 1900, p. 256; Müller, Engler Bot. Jahrb. XXXIV, 1903, p. 24.

faces with pronounced longer or shorter transv. costae (actually folds, like corrugated iron) and often with fine striae, interrupted by a median distinct linear or lanceolate pseudo-raphe, that of one valve parallel to that of the other; marginal wings (generally more obvious in the girdle- than the valve-view, best seen in transv. section (fig. 144, C)) traversed by horizontal canals (fig. 144, D) connecting the raphe with the interior of the frustule and separated by conspicuous partitions corresponding to the costae on the valve-faces (cf. p. 339). Girdle-view subrectangular,

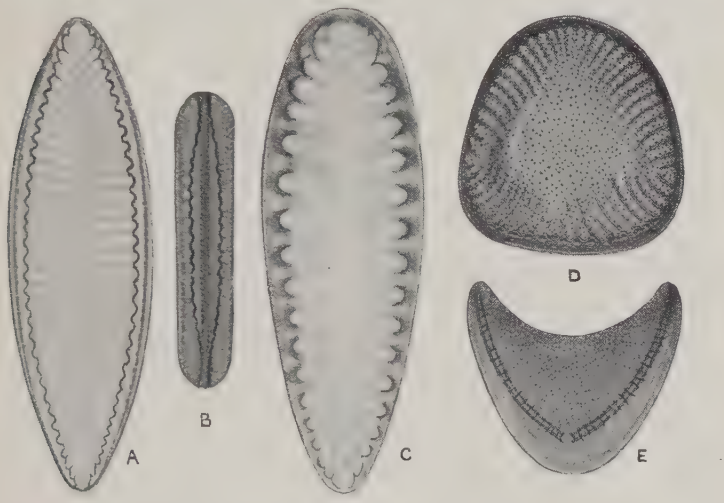

Fig. 166. A, *Surirella biseriata* Bréb., from Adel Bog, W. Yorks, valve-view. B, *S. linearis* W. Sm., from Mickle Fell, N. Yorks, girdle-view. C, *S. robusta* Ehrenb. var. *splendida* (Ehrenb.) V. H., from near Penzance, Cornwall, valve-view. D and E, *Campylodiscus Hibernicus* Ehrenb., from Baildon, W. Yorks; D, valve-view; E, view showing the saddle-shaped frustule. (All × 400.)

oblong, or cuneate; girdle sometimes with irregular longitudinal striations. Chromats. two, one against either valve, often connected by a transv. bridge; numerous pyrens.

There are eight Brit. freshwater sp. *S. biseriata* Bréb. (fig. 166, A; valves 100–170 l.) and *S. robusta* Ehrenb. (valves 160 -230 l.) are two of the largest and most frequent. Both are common Brit. plankton forms, especially the var. *splendida* (Ehrenb.) V. H. (fig. 166, C) of the latter. The much smaller *S. ovalis* Bréb. (valves 16–80 l.), with numerous vars., is also very abundant. *S. spiralis* Kütz. is remarkable for the twisting of the valves round the longit. axis; in this sp. G. S. West (1912, p. 325) has recorded the formation of eight thick-walled rounded-polygonal spores from the contents of a frustule.

Campylodiscus Ehrenberg, 1841. Frustules saddle-shaped with circular valves, which however appear irregularly circular owing to the curvature of the frustules. Sagittal axes of the two valves (including the pseudo-raphe) at right angles to one another; valves with usually short and often beaded costae arising from a thickened margin, the centre of the valve with irregular punctae. Presence of a raphe doubtful. Two chromats., without pyrens.

The genus, which is chiefly marine, is incompletely known. There are two Brit. freshwater sp., of which *C. Hibernicus* Ehrenb. (fig. 166, D, E) is general, but scarce; valve about 100 br.

CLASS V. CRYPTOPHYCEAE

The Cryptophyceae, which are apparently more strongly represented in the sea than in freshwaters, are as yet but very imperfectly known. Enough has come to light, however, to bring out clearly some of the essential characteristics and to show that much the same evolutionary sequence has been followed as in the other great flagellate-algal series. Its immediate affinities are obscure, but there are some striking resemblances with the Dinophyceae (Peridinieae)[1] and perhaps a remote relation to the Phaeophyceae. The Cryptophyceae may well have a common origin with the Dinophyceae, although at one time they were thought to be derived from forms like the Ochromonadales[2], with which there are some points of resemblance.

The naked motile individuals are developed in their most typical form in the Cryptomonadaceae and exhibit a pronounced dorsiventral construction, the cells being prominently flattened in the dorso-ventral plane, so that the cross-section is oval or elliptical (fig. 1, I, p. 22). When the individuals lie on one of their broader faces (side-view), the anterior extremity appears obliquely truncate or emarginate, whilst the dorsal margin is convex and the ventral margin usually flat or concave (figs. 1, J; 167, C). Passing over the anterior extremity, where it produces a more or less marked constriction, is a longitudinal furrow, which extends obliquely over the flanks to die out sooner or later without reaching the posterior end (fig. 167, E); in some genera (e.g. *Cryptomonas* (figs. 1, J; 167, A and C)) there is a tubular gullet extending from the anterior end of the furrow more or less deeply into the interior of the protoplast, but in others (e.g. *Cryptochrysis*[3], *Chroomonas* (fig. 167, E)) this is lacking. Two somewhat unequal cilia arise at the anterior end, either from the furrow or the ventral edge of the aperture of the gullet (fig. 167, C). The cilia are slightly band-shaped, with a thread-like termination, and arise from a basal granule which, in *Chilomonas*, has been shown to be connected by a delicate thread with the large nucleus[4]. The latter is usually situated near the posterior extremity (fig. 167, *n*). The periplast is firm and the cells are not metabolic.

[1] Pascher, 1914, p. 150; cf. also p. 397.
[2] cf. Pascher, Ber. Deutsch. Bot. Ges. xxix, 1911, p. 200.
[3] Pascher, ibid. p. 190.
[4] Ulehla, ibid. p. 285.

There are usually two large, and often lobed, parietal chromatophores, mostly apposed to the dorsal and ventral margins respectively (fig. 167, E), though sometimes there is only one; in a few cases the chromatophores are numerous and discoid. Their pigmentation is very variable, even in the same lot of material, but diverse shades of brown are probably the most frequent; apart from these, reddish, olive-green, and blue-green tints occur. Nothing is known about the nature of the pigments[1]. Rounded pyrenoid-like bodies often occur independently[2] of the chromatophores (fig. 167, *p*); usually there is one in the middle of the cell, but there may be several[3]. After active photosynthesis the products are stored as solid discoid granules, which in *Cryptomonas* give a blue coloration with iodine and appear to be some form of starch, whilst in other cases (e.g. *Cryptochrysis*) iodine colours them reddish or reddish-violet. These granules constitute a shell around the pyrenoids, as well as occurring over the inner surface of the chromatophores. A prominent contractile vacuole, which discharges into the furrow or into the gullet when present, is situated anteriorily on the dorsal side (fig. 1, J); in some species there is more than one. The furrow or gullet are often lined with small rod-shaped highly refractive granules, which are stated to be trichocysts.

Reproduction is effected by longitudinal division, generally during the motile phase, but in most species of *Cryptomonas* the dividing cells come to rest and are embedded in mucilage, often forming extensive palmelloid groups. Thick-walled cysts, with a membrane containing cellulose, are known in various Cryptomonadales.

As in other series of motile unicellular forms, there are interesting special developments. Thus, in the Nephroselmidaceae (e.g. *Protochrysis* (fig. 167, D))[4] the body is kidney- or bean-shaped and the two cilia are attached laterally, a little below the middle of the concave surface, the shorter being directed forwards, the longer trailing behind during movement; an eye-spot is situated just below the point of attachment of the cilia. In this family, moreover, the oblique furrow runs more or less transversely from the point of origin of the cilia[5]. Among the Crypto-

[1] According to Pascher, 1913, p. 96, they are probably similar to those of the Peridinieae.

[2] In *Rhodomonas*, however, they are embedded in the chromatophore (Zimmermann, Ber. Deutsch. Bot. Ges. XLI, 1923, p. 285).

[3] cf. Dangeard, Bull. Soc. Bot. France, LVIII, 1911, p. 449; Geitler, Rev. Algol. I, 1924, p. 361.

[4] Senn, Zeitschr. wiss. Zool. XCVII, 1911, p. 605; Pascher, ibid. C, 1912, p. 177; Pascher, Ber. Deutsch. Bot. Ges. XXIX, 1911, p. 191.

[5] There is an undoubted resemblance with the swarmers of Phaeophy-

monadaceae a number of colourless saprophytic types are known; *Chilomonas*, for example, is very like a colourless *Cryptomonas* and like it forms starch[1].

A small number of non-motile algal forms have been discovered which seem to represent modifications analogous to those found in other classes. The palmelloid Phaeocapsales (including Borzi's *Phaeococcus*[2] and Pascher's *Phaeoplax*[3] = *Phaeococcus marinus* Reinisch) reproduce by swarmers of the Cryptomonad type, in fact those of the marine *Phaeoplax* are almost identical in structure with a *Cryptochrysis*. Pascher[4] has described, from moorland pools, small free-floating tetrahedral cells (*Tetragonidium*) having a brown lobed chromatophore and reproducing by swarmers of the same kind, which he classes in the Cryptococcales (parallel with Chlorococcales, Heterococcales, etc.). No filamentous members of the class are at present known[5]. For *Phaeococcus* an isogamous sexual process is recorded, but sexuality seems to be lacking in the motile types. The genera mentioned in this paragraph are true Algae with firm cell-walls, so that here, as in the Heterokontae and Chrysophyceae, there is quite a gradual transition from flagellate to algal organisation.

The classification of the members of this class proposed by Pascher (1914, p. 158; cf. also 1913, p. 99) is as follows:

A. *Cryptomonadales*, in which the motile phase is dominant.
  Family 1. *Cryptomonadaceae*, with apical cilia and an oblique apical furrow, e.g. *Cryptochrysis* and *Chroomonas* without a gullet and with an ill-differentiated periplast; *Cryptomonas* and *Chilomonas* with a gullet and a distinct periplast.
  Family 2. *Nephroselmidaceae*, with lateral cilia and an equatorial furrow, e.g. *Protochrysis* (fig. 167, D).

B. *Phaeocapsales*, with a dominant palmelloid phase, e.g. *Phaeococcus*, *Phaeoplax*.

C. *Cryptococcales*, comprising motionless unicellular individuals; only genus *Tetragonidium*.

ceae, first pointed out by Pascher (ibid. p. 199); subsequently, however, the latter regarded this resemblance as of no phylogenetic significance (cf. Pascher, 1914, p. 153).

[1] The Zooxanthelleae, which live symbiotically within diverse Rhizopods, Radiolarians, etc., also belong to the Cryptomonadales.

[2] Borzi, Atti Congr. Bot. Internaz. Genova, 1892, p. 463. Regarding *Phaeococcus paludosus* W. & G. S. West and *P. planctonicus* W. & G. S. West, see p. 331.

[3] Reinisch, Ber. Deutsch. Bot. Ges. XXIX, 1911, p. 77; Pascher, ibid. p. 197.

[4] Pascher, 1914, p. 160.

[5] *Phaeothamnion* was at one time referred to this class, but has since been shown to belong to the Chrysophyceae (p. 334).

Up to the present only two genera of this class are known to occur in the British Isles, viz.

Chroomonas Hansgirg, 1885[1]. Unicell., motile, naked, with an ill-defined periplast, cilia about as long as the cell; individuals flattened, dorsiventral, with a convex dorsal and a concave ventral margin, anterior end oblique and emarginate, posterior end rounded; furrow often indistinct, not prolonged into a gullet, but trichocysts grouped much as in *Cryptomonas* stated to be present; cilia arising apically from edge of furrow. Chromats. blue or blue-green, parietal, at first single, later frequently two, often lobed; pyren. median; starch stored. Contr. vacs. discharging into the furrow. Reprod. by longit. div. of individuals that have come to rest and secreted an envelope of mucilage.

C. Nordstedtii Hansg. (*Cryptomonas Nordstedtii* (Hansg.) Senn) (fig. 167, E), the only Brit. sp., is so far only recorded from Harborne, Staffordshire (Grove, 1920, p. 2); cells 9–16 l.

Cryptomonas Ehrenberg, 1838[2]. Unicell., motile, naked, with a firm periplast; cells dorsiventral, in shape like those of *Chroomonas*, anterior end more or less oblique and often emarginate; furrow oblique, passing over the anterior end and prolonged into

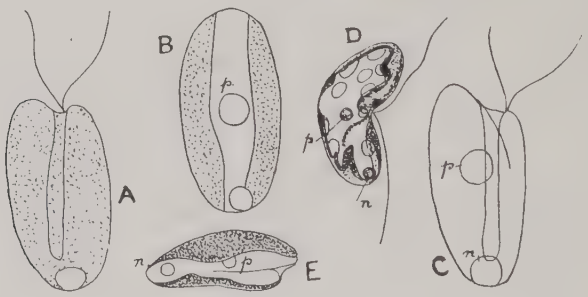

Fig. 167. A–C, *Cryptomonas anomala* Fritsch, from Houghton-on-the-Hill, Leicester (×1050); A and C, side-view; B, view from the dorsal surface. D, *Protochrysis phaeophycearum* Pascher (after Pascher, ×900). E, *Chroomonas Nordstedtii* Hansg. (after Pascher, ×975). *n*, nucleus; *p*, pyrenoid.

a curved gullet which extends for a varying distance towards the posterior end and is lined with "trichocysts"; cilia arising from ventral margin of gullet. Chromats. brown or olive-green, parietal, one or more usually two, generally apposed to the dorsal

[1] Hansgirg, Bot. Centralbl. XXIII, 1885, p. 230, and Prodr. d. Algenfl. v. Böhmen, II, 1892, p. 167; Zimmermann, loc. cit. p. 286.

[2] Dangeard, Le Botaniste, I, 1889, p. 8, and XI, 1910, p. 208; Pascher, 1913, p. 105; Fritsch, 1914, p. 346.

and ventral surfaces, but sometimes occupying the flanks; pyren. median; starch or allied carbohydrate (reddish with iodine) stored. Contr. vacs. 1–3, discharging into the gullet. Reprod. by longit. div., usually of resting individuals embedded in mucilage, often forming extensive palmelloid groups or, as a result of one-sided mucilage-production, rough dendroid groups of cells borne on short thick stratified mucilage-stalks. Endogenous cysts also known.

Sp. of this genus are of common occurrence, frequently favouring waters rich in organic substance. Of the four Brit. freshwater sp., *C. ovata* Ehrenb. (20–80 l.) (fig. 1, J) is the commonest. *C. erosa* Ehrenb. (15–32 l.), with a shorter gullet, has also been recorded several times. *C. anomala* Fritsch (21–24 l.) (fig. 167, A–C), as yet only known from Leicestershire, is peculiar in the placing of the two chromats. against the flanks of the individual.

Many sp. of *Cryptomonas* exhibit a characteristic swaying of the individuals, first to one side and then to the other, during movement.

CLASS VI. DINOPHYCEAE (PERIDINIEAE)

The members of this class play a very important rôle as plankton-organisms, both in the sea and in freshwaters, and have at times been known to occur in such large numbers as to give a definite coloration to smaller pieces of water[1]. The freshwater forms exhibit greater uniformity and are less elaborate in structure than the marine ones. Whilst the large majority of Dinophyceae are motile unicells, we owe to Klebs[2] and Pascher[3] the discovery of a number of types which show that here also evolution of a sedentary phase has not been lacking. The establishment by Pascher of the four series Dinoflagellata, Dinocapsales, Dinococcales, and Dinotrichales indicates without further words that the Dinophyceae exhibit the same essential types of organisation as the other classes hitherto considered.

The motile individuals are commonly more or less subcircular or ovoid in outline (figs. 168, C; 169) and are usually flattened, so that the end-view appears subelliptical or reniform (cf. fig. 170, C, D). In most cases they are provided with a well-marked and often elaborate envelope consisting largely of cellulose[4], but in a few genera (e.g. *Gymnodinium* (fig. 169, C)) the membrane is lacking or indistinct. The protoplast, which is bounded by a firm plasma-membrane, is provided with two furrows, the one transverse and the other longitudinal (fig. 168, C), and this structure, which is eminently characteristic of practically all the members of the class, is exhibited also by the overlying envelope when that is present (fig. 170, E–F). The transverse furrow is usually well marked and, except in *Hemidinium* (fig. 169, B–C), completely encircles the cell, separating the *apical* half which is directed forwards during movement from the *antapical* half[5]. The longitudinal furrow, which is not

[1] cf. Naumann, Archiv f. Hydrobiol. u. Planktonkunde, XIII, 1922, p. 679. There are also various records of the phenomenon of "red snow" being due to Peridinieae, cf. Suchlandt, Ber. Deutsch. Bot. Ges. XXXIV, 1916, p. 242.

[2] Verhandl. Nat.-Med. Ver. Heidelberg, XI, 1912, p. 369.

[3] Pascher, 1914, p. 151; 1918, p. 395.

[4] Mangin, Comptes Rendus, Paris, CXLIV, 1907, p. 1055; and Internat. Rev. Hydrobiol. u. Hydrogr. IV, 1911, p. 44.

[5] In most freshwater Peridinieae the apical half is slightly larger than the antapical one, but in *Amphidinium* it is quite minute in comparison with the latter.

uncommonly rather broad and generally less distinct[1], occurs on the ventral flank of the flattened cell (cf. fig. 169, C). It is often confined to the antapical half opening into the transverse furrow at its upper end, or it may continue across the latter for a varying distance into the apical half (fig. 170, A, F); in *Gonyaulax apiculata* it extends right up to the anterior extremity, but this is unusual. In most cases the transverse furrow follows a more or less horizontal course, the portions to right and left of the longitudinal furrow being at practically the same level; but there is often a slight spiral trend, and in *Spirodinium* the transverse furrow appears as a steep spiral and the two sections of it visible on the ventral surface are far apart, though linked by the longitudinal furrow.

At the point where the furrows meet two cilia emerge through an aperture in the membrane (figs. 168, C; 169, A). One of these, taking the form of a narrow undulating band, occupies the transverse furrow. When the individual is viewed from the ventral surface with the apical half directed forwards, this transverse cilium extends from its point of origin to the right, along the transverse furrow (figs. 169, A; 1, E), and, passing round the dorsal surface (cf. fig. 169, D), reappears again on the left-hand side to terminate close to its starting-point. It thus encircles the individual, but is confined to the furrow and does not project in any way. The second cilium is a fine thread, often considerably longer than the body of the cell, and is directed backwards during movement (figs. 168, 169); its proximal portion lies in the longitudinal furrow, but the greater part projects into the surrounding water. The transverse cilium exhibits undulating movements believed to cause the rotation observable during the forward progression of the individual which is probably mainly brought about by the longitudinal cilium; the latter is usually stretched straight out.

In a certain number of the Dinoflagellata, if an envelope is present at all[2], it is relatively delicate and little or no structure can usually be made out in it. These forms are conveniently classed as Gymnodiniaceae (cf. figs. 1, E; 168, C; 169). In the Peridiniaceae, however, there is a coarse and often richly sculptured envelope, composed of the apical *epivalve*, the antapical *hypovalve*, and the intervening *girdle* occupied by the transverse

[1] In some species of *Gymnodinium* (e.g. *G. pulvisculus* Klebs) it is scarcely distinguishable.

[2] According to Woloszynska (Bull. Acad. sci. Cracovie, mat.-nat. Kl., sér. B, 1917, p. 114) there is a delicate envelope composed of numerous polygonal plates even in *Gymnodinium*, whilst G. S. West (1916 *a*, p. 61, footnote) and others have recorded indications of a plate-like structure in the membrane of species of *Glenodinium*.

furrow (cf. fig. 170); each of these is made up of a series of plates, the number and arrangement of which is an important aid in classification (cf. *Peridinium*, p. 401, and *Ceratium*, p. 402). Adjacent plates of the envelope overlap by their knife-like margins which are firmly cemented together, the sutures between them being often but not always clearly recognisable[1]; frequently the plates are connected by prominent *intercalary bands* (cf. fig. 170, A–D)

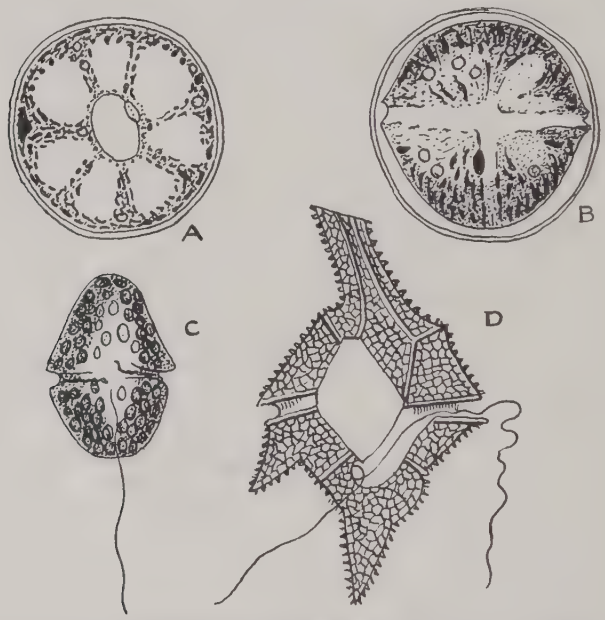

Fig. 168. A–B, *Hypnodinium sphaericum* Klebs (after Klebs, ×300). B, cell preparing to divide. C, *Gymnodinium aeruginosum* Stein (after Schilling), ventral surface. D, *Ceratium cornutum* Clap. and Lachm. (after Schilling), ventral surface.

which are commonly striated and which seem to widen in older individuals, thus admitting of some slight increase in the dimensions of the cell[2]. In many species the plates are ornamented by numerous areolations and the margins are frequently produced into ridges or beset with teeth or small spines (fig. 171); in particular the rims of the girdle are often developed as ridges (fig. 170, A, E) making the transverse furrow especially conspicuous. The plates of the wall are usually pierced by pores,

[1] Treatment with warm dilute potash generally causes the plates to fall apart.

[2] cf. also Mangin, loc. cit. 1911, p. 47. For other views as to the intercalary bands, see Kofoid, Archiv f. Protistenkunde, XVI, 1909, p. 31.

one of which not uncommonly occupies the centre of each areolation, whilst in many cases there is a conspicuous pore at the apex of the epivalve. It seems that the cytoplasm projects through these pores, and it is possible that the sculpturing seen on the external surface of the envelope is formed by this extra-membranous protoplasm[1].

The protoplast, whose distinctive furrowing has already been mentioned, commonly consists of an outer denser and more or less granular region harbouring the chromatophores, and an inner portion that contains nucleus and vacuoles (fig. 1, E). The chromatophores[2] are usually numerous (fig. 168, C) and generally more or less discoid, but in some cases they are rod- or band-shaped. They exhibit varied pigmentation, though shades of dark yellow and brown are the commonest. Three pigments have been extracted from them, viz. the water-soluble brownish-red phycopyrrin, the dark red peridinin, and the yellowish-green chlorophyllin, the two latter soluble in alcohol; the different tints are stated to be produced by their varied aggregation. A few blue-green forms are also known (e.g. *Gymnodinium aeruginosum*) which are said to contain phycocyanin. Reserve-food is stored as starch and oil, the latter often of a yellowish or reddish colour. Most of the freshwater Peridinieae appear to be holophytic, but there are a number of colourless forms whose nutrition is saprophytic or holozoic.

The nucleus[3] is usually large and conspicuous and either presents a finely granular structure or exhibits numerous very fine threads, which probably represent the chromatin; the latter type is especially distinctive of many Dinoflagellata. Structures of the nature of contractile vacuoles (pusules) are known in the marine genera, but have hitherto not been observed in the fresh-water types. Some species possess a well-defined eye-spot which lies at the surface of the protoplast in the longitudinal furrow (fig. 1, E), but in many cases it is lacking.

Multiplication is effected by division of the cells into two, and this usually takes place along the longitudinal axis. In a few cases (*Gymnodinium*, *Ceratium*) it occurs during movement. In the division of *Ceratium* the elaborate envelope splits (fig. 171, C), the line of rupture always running between definite plates; as the enlarging protoplast divides, the two portions exposed by the rupture of the parent-envelope gradually assume the characteristic shape of the species (fig. 171, D), but it is not until

[1] cf. Schütt, Jahrb. Wiss. Bot. XXXIII, 1899, p. 598.

[2] The chromatophores of Dinophyceae are very delicate and readily undergo disorganisation.

[3] cf. Klebs, loc. cit. p. 416.

some little time after division is complete that the missing plates of the membrane are gradually formed. In this case therefore the daughter-individuals receive part of their membrane from the parent.

In the majority of the Dinoflagellata, however, division is effected during a sedentary phase. Cessation of movement is followed by a more or less marked contraction of the protoplast. Division may then follow at once, the two new individuals being set free by the rupture of the parent's membrane (e.g. *Peridinium tabulatum*) or, more frequently, the contracted and spherical protoplast acquires a new membrane (fig. 170, G), and the old one is discarded[1]. This state may last for a varying period according to the species, but in most cases, given favourable conditions for development, it is merely a passing phase, the protoplast soon dividing to form new motile individuals. These thin-walled cysts are usually more or less spherical in shape, but in *Cystodinium* for example, where the motile stages are indistinguishable from *Gymnodinium*, they are lunate or produced into horns[2]. In this genus, moreover, the encysted state is of relatively long duration.

Resting cysts, with a thick membrane and abundant food-reserves and often of a somewhat characteristic shape (cf. fig. 171, B), are known for a number of Peridinieae and are no doubt of wide occurrence, constituting the method of survival during the unfavourable period of the year[3]. In *Gymnodinium* they are frequently provided with a mucilage-envelope.

The existence of other methods of reproduction is still very uncertain. Various observers have described a sexual fusion, either between normal individuals (*Ceratium*[4]) or between special small isogamous swarmers showing the structure of a *Gymnodinium* (in *Hypnodinium*[5]). These records, however, require fuller investigation.

The forms above considered mainly belong to the Dinoflagellata in which the motile phase is dominant and which are the only ones so far recorded from Great Britain. Of the sedentary types, the Dinococcales are all azoosporic, unless we follow Pascher (1918, p. 396) and transfer to them the above-mentioned *Cystodinium* which would constitute a zoosporic member. Among the completely motionless Dinococcales are

[1] cf. especially G. S. West, New Phytol. VIII, 1909, p. 182 et seq.

[2] It is probable that some of the described species of *Reinschiella* (cf. p. 127) are the horned cysts of such Peridinieae.

[3] cf. West, loc. cit. p. 193.

[4] Zederbauer, Ber. Deutsch. Bot. Ges. XXII, 1904, p. 1.

[5] Pascher, 1914, p. 152.

some which still develop the distinctive furrows in the protoplast prior to division (e.g. *Hypnodinium* (fig. 168, A–B)), whilst in *Phytodinium* even these characteristics of the motile phase are lacking[1]. Pascher's *Dinothrix*[2], the only filamentous member of Dinophyceae as yet known, possesses rather coarse, little branched threads composed of barrel-shaped cells with numerous discoid yellow-brown chromatophores; multiplication is effected by fragmentation and by *Gymnodinium*-like swarmers. It is to be hoped that Pascher's brief diagnosis will soon be amplified by a more detailed description.

There can be no question that this well-defined class has a long history in the past. As a matter of fact an undoubted species of *Peridinium* has been described from the Cretaceous. There appears to be a distinct affinity with the Cryptophyceae, first clearly brought out by Pascher (1914, p. 149) and accepted by most recent writers on the class. Such forms as *Protochrysis* (cf. p. 388) evidently show many points of similarity with *Gymnodinium*, both in general organisation as well as in the pigmentation of the chromatophores and the products of photosynthesis. Probably related to the Dinophyceae are a series of forms (Prorocentraceae) comprising motile unicells, often with a bivalved cell-membrane and a more or less marked dorsiventral organisation, which however lack the characteristic furrows of the Peridinieae. The Prorocentraceae are largely marine and thus outside the scope of this work, but it is not improbable that the three series Prorocentraceae, Cryptophyceae and Dinophyceae may have originated from a common stock. A relationship with Bacillariales, such as was formerly entertained, is at least unlikely.

Only five genera of Dinophyceae have so far been found in British freshwaters, all of them belonging to the Dinoflagellata. The following key for their determination is but slightly modified from the keys given by Lemmermann[3] and Schilling[4], to whom we owe the most recent systematic treatment of the freshwater members of the class:

A. Cells naked or provided with a membrane, not evidently composed of distinct plates — *Gymnodiniaceae*

a. Transverse furrow only extending round half the cell — *Hemidinium*

b. Transverse furrow completely encircling the cell

[1] Klebs, loc. cit. p. 406.
[2] Pascher, 1914, p. 160.
[3] Lemmermann, 1910, p. 563 et seq.
[4] Schilling, Dinoflagellatae (Peridinieae) in Pascher, Suesswasserfl. III, 1913.

1. Cells naked, cysts generally with a mucilaginous membrane *Gymnodinium*

2. Cells with a smooth membrane, cysts thick-walled *Glenodinium*

B. Cells with a membrane obviously composed of a series of coarse plates *Peridiniaceae*

a. Envelope not produced into horns *Peridinium*

b. Envelope produced into horns *Ceratium*

The above classification into two families is purely one of convenience, since recent observations[1] indicate that no sharp distinction can be drawn between them.

Hemidinium Stein, 1883. Cells with a delicate structureless cellulose-wall, rounded or ellipsoid in form, with rounded poles, and markedly flattened on the dorsal and ventral surfaces; transv. furrow originating in the middle of the ventral and terminating in the middle of the dorsal surface, only encircling half the cell; longit. furrow confined to the antapical half. Chromats. numerous small plates in the peripheral cytopl.; no eye-spot; nucleus posterior; reddish-brown oil-drops often present. Resting cysts spherical with a firm membrane.

H. nasutum Stein (fig. 169, B, C) has been recorded from two localities in the neighbourhood of Birmingham (Grove, 1920, p. 9), but may well have a wider distribution; cells 24–28 l. and 16–17 br.

Gymnodinium Stein, 1883. Cells in the motile phase naked (or with a delicate membrane composed of numerous hexagonal plates?), in general outline subcircular or oval, with bluntly rounded, more rarely pointed poles, end-view subcircular; transv. furrow dividing the body into nearly equal halves, horizontal or faintly spiral; longit. furrow usually confined to the antapical half, but sometimes projecting a short distance into the apical half, occasionally very indistinct. Chromats. generally in the form of rounded discs, numerous, yellow to reddish-brown in colour, sometimes green, blue-green, or blue, absent in some sp.; eye-spot sometimes present; nucleus variable in position. Multipl. by div. during movement, usually longit., rarely transv. Resting cysts with a mucilaginous envelope or a firm membrane. Protrusion of pseudopodia from the region of the transv. furrow has been observed in some sp.

Sp. of this genus are widely distributed, but not usually abundant; they favour small pieces of stagnant water harbouring a lot of macroscopic growth. Four are known from British freshwaters. *G. paradoxum* Schilling (39·5 l.; 34·5 br.) (fig. 169, A) has been found

[1] cf. Woloszynska, loc. cit.

in the plankton of the English and Scotch lakes, whilst a larger var. is recorded from the Irish lakes; the longit. furrow is scarcely recognisable, but a conspicuous eye-spot occupies its place just below the point of attachment of the cilia. *G. aeruginosum* Stein (33 34 l.;

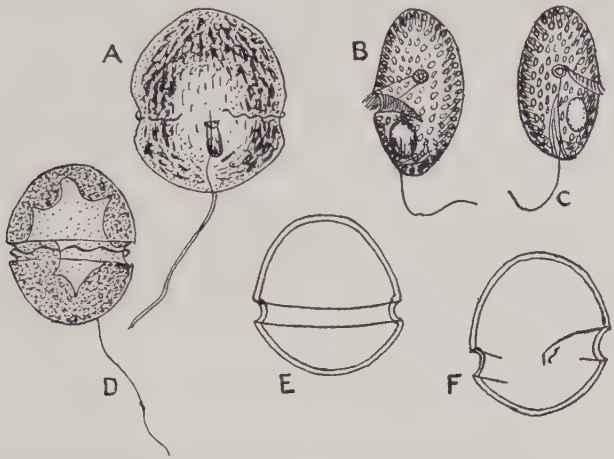

Fig. 169. A, *Gymnodinium paradoxum* Schilling (after Schilling), ventral surface. B–C, *Hemidinium nasutum* Stein (after Lemmermann); B, dorsal, and C, ventral surface. D–F, *Glenodinium uliginosum* Schilling (after G. S. West, × 500), from Sutton Park, Warwickshire; D, young individual developed from a cyst, dorsal surface; E and F, empty membranes.

21–22 br.) (fig. 168, C), with blue-green chromats., has been recorded from ponds in Warwickshire. *G. Vorticella* Stein, one of the colourless forms, has been found in a pond near Newcastle (Griffiths, 1923, p. 191).

Glenodinium (Ehrenberg) Stein, 1883[1]. Cells in the motile phase with a firm and distinct membrane, usually smooth and structureless, but sometimes showing delicate suture-lines evidently demarcating plates similar to those of *Peridinium*; cells in general outline subcircular or sometimes elongate, usually with rounded poles, end-view elliptical or reniform; transv. furrow in the middle or, not uncommonly, nearer the posterior end of the cell, slightly spiral; longit. furrow confined to the antapical half, often very distinct. Chromats. numerous[2], discoid, yellow to dark brown in colour, sometimes absent; horseshoe- or rod-shaped eye-spot in the longit. furrow of some sp. Resting cysts with a firm membrane.

[1] West, loc. cit. p. 181.

[2] G. S. West (loc. cit. p. 185) records only two or three lobed parietal chromats. in the young individuals of *G. Pulvisculus*.

Of the three Brit. freshw. sp., *G. Pulvisculus* (Ehrenb.) Stein (*Peridinium Pulvisculus* Ehrenb.) is the smallest (26–27 l.; 22 br.) and appears to occur commonly, but not abundantly, in the plankton of pools and lakes; in this sp. the apical and antapical halves are equal. *G. uliginosum* Schilling (36–43 l.; 34–38 br.; cysts 33–40 br.) (fig. 169, D–F) is not uncommon among submerged *Sphagnum* in bogs and swamps; its biology has been thoroughly investigated by G. S. West. *G. cinctum* (Müll.) Ehrenb. (fig. 1, E) is a rare plankton form (43 l.; 40 br.), with a prominent horseshoe-shaped eye-spot.

Peridinium Ehrenberg, 1830[1]. Cells with an elaborate membrane, clearly composed of a definite number of regularly

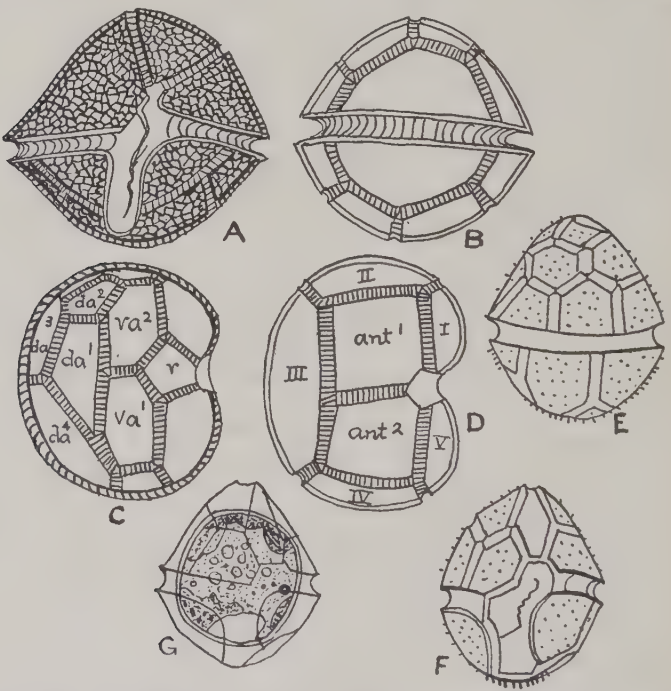

Fig. 170. A–D, *Peridinium cinctum* Ehrenb. var. *Lemmermanni* G. S. West (after G. S. West, × 500), from Sutton Park, Warwickshire; A, ventral, and B, dorsal views; C, epivalve; D, hypovalve. *r*, rhomboidal plate; *va*[1] and *va*[2], ventral apical plates; *da*[1] and *da*[2], dorsal apical plates; *da*[3] and *da*[4], two of the precingular plates; *ant*[1] and *ant*[2], antapical plates; I–V, postcingular plates. E–G, *P. anglicum* G. S. West (after G. S. West, × 500), from Sutton Park, Warwickshire; E, dorsal and F, ventral views; G, cyst within old wall.

[1] Schütt, Sitz.-Ber. Akad. Wiss. Berlin, 1892, p. 377; Kofoid, Archiv f. Protistenkunde, XVI, 1909, p. 25; West, loc. cit. p. 186; Virieux, Comptes Rendus Soc. Biol. LXXVI, 1914, p. 534.

arranged plates (cf. below), in general outline ovoid or subcircular, sometimes produced into two or more spiny teeth at one or both extremities; end-view invariably reniform (fig. 170, C, D) owing to the slight concavity of the ventral surface; transv. furrow faintly spiral, broad, and usually with projecting rims, situated slightly but distinctly below the middle of the body, so that the antapical half is smaller than the apical (fig. 170, E); longit. furrow broad and evident, extending beyond the transv. one for a variable distance into the apical half of the individual. Chromats. numerous small rounded discs, pale- or dark brown in colour; stigma usually absent. Resting cysts spherical, with a simple, but firm membrane (fig. 170, G).

The plates of the epivalve (usually 11–14) are more numerous than those of the hypovalve (almost invariably seven). In the former one distinguishes the plates immediately adjacent to the apex as the *apical plates* (fig. 170, C, va^1, va^2, da^1, da^2), whilst those adjacent to the girdle are known as the *precingular plates* (da^3, da^4, etc.); of the latter there are always seven, whilst the number of apical plates varies. In many sp. of the genus one finds on the dorsal surface of the epivalve from 1–3 plates which intervene between the apicals and are spoken of as *intercalary plates*. The actual apex of the epivalve may be occupied by a single plate (e.g. *P. bipes* Stein), but is more usually covered by several plates (e.g. *P. tabulatum* Clap. & Lachm.). Occupying the middle of the ventral surface, and extending from the upper end of the longitudinal furrow either to the apex or close up to the apex of the epivalve, is a characteristic *rhomboidal plate* ("Rautenplatte" of the Germans (fig. 170, C and F, *r*)); this is one of the apical plates.

The hypovalve similarly consists of two *antapical plates* (fig. 170, D, *ant*) and five *postcingular plates* (I–V), adjacent to the girdle; the former cover the posterior extremity of the individual, while the latter are interrupted on the ventral surface by the longit. furrow. The nomenclature of the plates here adopted is that introduced by Kofoid (loc. cit. p. 40) which has many advantages over the older systems; he advocates a designation of the individual plates of each series by numbers, starting from the longitudinal furrow and following the direction of the transverse cilium. There seems no doubt that the transverse and longitudinal furrows of the membrane are likewise occupied by a series of plates, but these are not easily recognisable and are at present imperfectly known. The girdle often becomes detached as one ring-shaped piece.

It is usual to group the sp. of this genus in two sections, viz. *Poroperidinium* in which the apical pole is prolonged into a more or

less distinct tip which is pierced by an open pore, and *Cleistoperidinium* in which the apical pole is bluntly rounded and destitute of the pore. The genus is well represented in Brit. freshwaters and there are records of 15 sp. Among the most widely distributed are *P. Willei* Huitfeldt-Kaas, *P. cinctum* Ehrenb. (fig. 170, A–D), *P. tabulatum* (Ehrenb.) Clap. & Lachm. (*Glenodinium tabulatum* Ehrenb.), and *P. inconspicuum* Lemm.; of these the first two belong to the section *Cleistoperidinium* and, like *P. tabulatum*, are conspicuous members of the plankton, though *P. cinctum* is also met with in small ponds and ditches. Another plankton-sp., *P. Westii* Lemm., is only known from the Scottish lochs. *P. inconspicuum* is one of the smallest sp. (15 18 l.; 12–15 br.), whilst *P. Willei* is one of the largest (51–61 l.: 53–64 br.). The former sp. is distinguished by the delicate, not ornamented, plates of which its wall is composed. In *P. tabulatum*, *P. Willei*, *P. cinctum*, and *P. Westii* the plates are provided with prominent areolations and connected by transv. striated intercalary bands, whilst in *P. anglicum* G. S. West (50–58 l.; 42 48 br.) (fig. 170, E–G) the plates bear numerous fine spines. A closely allied sp., *P. Marssonii* Lemm., distinguished from the last by its concave plates, is not uncommon in certain kinds of pools (Griffiths, 1923, p. 188 et seq.).

G. S. West has contributed valuable observations on the periodicity of some of the lowland sp. and the conditions governing cyst-formation.

Ceratium Schrank, 1793[1]. Cells with an elaborate membrane composed of a definite number of areolated plates, connected by rather narrow sutures, and with a large rhombic unsculptured hyaline area on the middle of the ventral surface (figs. 168, D; 171, A); ventral area probably homologous with what has above been called the longitudinal furrow of *Peridinium* (cf. Kofoid, loc. cit. p. 29). Cells asymmetric, strongly flattened in the dorso-ventral plane, produced into one apical and two or three antapical horns of more or less considerable length; transv. furrow nearly horizontal in its course, but interrupted by the ventral area, and dividing the body into two approximately equal, but dissimilar halves; longit. furrow confined to the antapical half, extending in an oblique direction from the transv. furrow towards the antapical pole along the edge of the ventral area; wall composed of apical, precingular, postcingular, and antapical plates as in *Peridinium*, the apical horn being formed

[1] Lauterborn, Zeitschr. wiss. Zool. LIX, 1895, p. 167; Zederbauer, loc. cit.; West, loc. cit. p. 192; Bachmann, 1907, p. 55; Kofoid, Zool. Anzeiger, XXXII, 1907, p. 177, and Bull. Mus. Comp. Zool. Harvard, LII, 1909, p. 213; Krause, Internat. Rev. Hydrobiol. u. Hydrogr. III, 1910, p. 181; Werner, Ber. Deutsch. Bot. Ges. XXVIII, 1910, p. 103; Joergensen, Monogr. d. Gatt. *Ceratium* Schrank, Leipzig, 1911; Huber and Nipkow, Zeitschr. f. Bot. XIV, 1922, p. 337, and Flora, CXVI, 1923, p. 114.

by a number of apical plates, whilst of the antapical horns one arises from the single antapical plate, the others from one or two postcingular plates. Chromats. small, discoid, yellow-brown; stigma absent; cytoplasm often with reddish oil-drops. Multipl. by div. during movement (cf. p. 395). Resting cysts thick-walled, with a number of blunt processes (fig. 171, B); with reference to their germination, see especially Huber and Nipkow (1922).

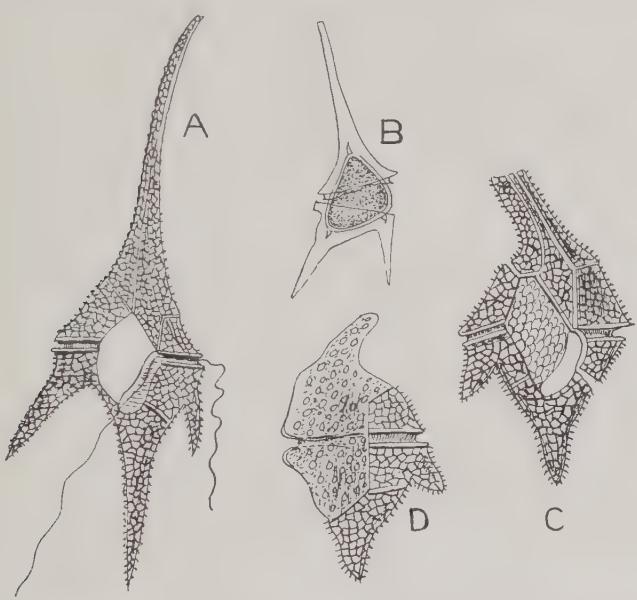

Fig. 171. A, *Ceratium hirundinella* O. F. M. (after Schilling), 4-horned form, ventral surface. B, the same (after G. S. West, × 150), 3-horned form, with cyst. C–D, *C. cornutum* Clap. & Lachm. (after Schilling, from Oltmanns); C, early stage in division; D, young individual assuming the mature shape.

Of the four sp. recorded from Brit. freshwaters, *C. hirundinella* O. F. M. (*C. macroceras* Schrank) (fig. 171, A, B) is an exceedingly abundant and typical constituent of the plankton of all larger pieces of water; according to Griffiths (1923, p. 204) it is almost always associated with deep water, and this is attributed to the presence of sediments lying in a region poor in oxygen. The cells are provided with long horns and vary very much in size, the largest individuals reaching as much as 400 μ in length. The antapical horns are two or three in number and, both in this respect as well as in the relative lengths of the different horns and their size as compared with the main body of the cell, there is a great deal of variability. Continental

observations on the occurrence of this ubiquitous sp.[1] have frequently demonstrated a certain periodicity in the appearance of 3- and 4-horned forms, but this has not been noted in Gt Britain (cf. West, 1916 *a*, p. 437). *C. cornutum* Clap. & Lachm. (fig. 168, D), a less graceful sp. with a more massive body and the apical horn inclined obliquely to the long axis of the cell, whilst the antapical horns are relatively short, is likewise widely distributed in the plankton of our lakes, but is also encountered in ponds; cells 97–150 l. and 48–75 br. According to Schilling (loc. cit. p. 54) this sp. is dependent on low temperature and adequate oxygen-supply. The much rarer *C. curvirostre* Huitfeldt-Kaas, which appears to be confined to the plankton, is characterised by the sickle-shaped curvature of the apical horn.

[1] cf. the summaries given by Bachmann, Mitteil. Naturf. Ges. Luzern, VI, 1911, p. 68; Lemmermann, 1910, p. 643; and Schilling, loc. cit. p. 57.

CLASS VII. CHLOROMONADALES

This appears to be but a very small class comprising a few highly specialised unicellular flagellate types of relatively large dimensions, none of which has yet been adequately studied[1]. Unlike the Chrysomonadales or Cryptomonadales no simply organised motile forms are known, nor have any palmelloid or filamentous members so far come to light. Whether the former are extinct, or the latter have never been evolved, only further research can show. The numerous discoid chromatophores (fig. 172, A) have a bright green tint, of a different shade to that of the Heterokontae, but, as there, due to an excess of xanthophyll, so that a blue-green colour is obtained with hydrochloric acid. Food-reserves are stored as oil. For these reasons an affinity with the Heterokontae has been assumed, but there is no other evidence pointing in that direction, and with our present knowledge the Chloromonadales are best regarded as an isolated class of uncertain affinities.

The individuals have two apically inserted cilia (fig. 172), one of which is directed forwards, while the other trails behind along the ventral surface which often exhibits a distinct groove. There is usually a complicated system of contractile vacuoles near the anterior end. Reproduction is effected by longitudinal division of the resting individuals, which become enveloped in copious mucilage. Cysts are also recorded.

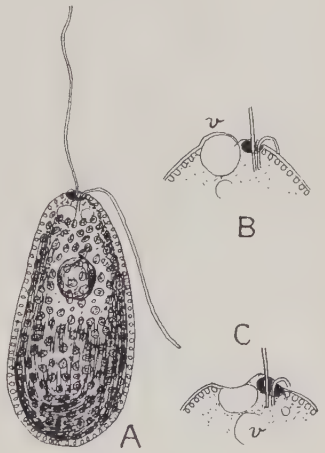

Fig. 172. *Vacuolaria virescens* Cienk. (after Senn, from Engler-Prantl, Natürl. Pflanzenfam.); A, motile individual (×590); B and C, anterior extremity greatly enlarged, to show the vacuolar system (*v*).

The only member of the class so far known to occur in the British Isles is

Vacuolaria Cienkowski, 1870[2]. Unicellular, motile, naked,

[1] The most recent account of the group is that of Pascher (1913, p. 175); cf. also Lemmermann, 1910, p. 478.

[2] Cienkowski, Archiv f. mikroskop. Anat. VI, 1870, p. 426; Klebs, Zeitschr. wiss. Zool. LV, 1893, p. 392; Dangeard, Le Botaniste, XI, 1910, p. 184.

with a very delicate but often distinct periplast, highly metabolic; movements slow, accompanied by continuous rotation; individuals when at rest ovoid or pyriform, slightly dorsiventral, with a broad rounded posterior and a narrower anterior end. Nucleus large and distinct, a little above the middle; chromats. numerous, discoid; contr. vacs. anterior, several, uniting to form one or two vesicles which discharge to the exterior (fig. 172, B and C); cilia two, coarse, almost equal, arising from a slight apical depression; no eye-spot. Reprod. by div. (cf. above). Cysts spherical with a thick mucilage-envelope.

V. virescens Cienk. (fig. 172) has in recent years been twice recorded from the Brit. Isles; cells 50–160 l. It is probably widely distributed, but as it usually occurs as solitary individuals and tends to be a mud-form, it is easily overlooked.

CLASS VIII. EUGLENINEAE

The Euglenineae represent another class of highly differentiated Flagellates whose origin is obscure. Like the Chloromonadales, they do not appear to have evolved beyond the phase of the ordinary motile individual and its immediate derivatives. There are no "algal" members of this class. The Euglenineae, however, are extremely successful at the present day, playing a considerable rôle in waters rich in organic nutriment and in those harbouring abundant vegetation. Not uncommonly they occur in such numbers as to give a characteristic coloration to the water, green for example in the case of *Euglena viridis* Ehrenb. (fig. 1, H), red in the case of *E. sanguinea* Ehrenb., or brown as in that of species of *Trachelomonas*[1].

In the ordinary state the individuals are motile with the help of one, or more rarely two (e.g. *Eutreptia* (fig. 173, G)) long and rather thick apical flagella: the accounts of their structure are contradictory[2]. The flagella are easily seen in the living organism, but are frequently cast off in preserved material. While many Euglenineae swim freely, others chiefly exhibit a creeping movement in contact with some substratum (e.g. *Peranema*, some *Euglenas*). The shape of the individuals is very diverse, but they are often approximately round in cross-section, though very prominently flattened in *Phacus* (fig. 173, H, I). The bounding layer or periplast is relatively soft in many species of *Euglena*, as well as in *Trachelomonas*, and in such cases the individuals, during life, show very marked metaboly, especially at times when active movement with the help of the flagellum is not taking place. Many Euglenineae (*Lepocinclis* (fig. 173, C, D), *Phacus*, many *Euglenas* (fig. 173, A, B)), on the other hand, have a rigid periplast that does not admit of change of shape; in such cases it frequently exhibits a characteristic longitudinal or spiral striation (fig. 173, D, F, I). The posterior end of the individual is commonly drawn out into a more or less sharply demarcated point or spine.

There are mostly several or even numerous chloroplasts which are pure green (fig. 173); in shape they are usually either discoid, lobed, or band-like, the last-named being occasionally arranged in

[1] cf. Zacharias, Forschungsber. Biol. Stat. Plön, x, 1903, p. 300; Naumann, Bot. Notiser, 1911, p. 245, and 1913, p. 249.

[2] cf. Dellinger, Journ. Morph. xx, 1909, p. 190; Hamburger, Sitzber. Heidelberg Akad. Wiss. 1911, No. 4 (cited from Oltmanns, 1922, p. 45).

characteristic stellate groups (*Euglena viridis* Ehrenb. (fig. 1, H)). The products of assimilation appear as solid, often large, granules of *paramylon*[1] of very diverse shape (discs, rods, rings, etc. (cf. fig. 173)) which is generally constant for the species. Paramylon is a polysaccharide which fails to stain with iodine or chlor-zinc-iodide, but is dissolved both by concentrated sulphuric acid and by potash; formalin often brings about a gradual solution. When the grains are subjected to dilute (6 per cent.) potash they swell and then often exhibit a concentric stratification (sometimes visible without special treatment) like that of starch-grains, which they also resemble in being doubly refractive. The central portion of the grains appears to be less dense than the peripheral. In many species of *Euglena* the paramylon-grains arise in direct contact with the chloroplasts, but in other cases (e.g. *Phacus*, *Lepocinclis*) there is no such definite relation, and it would seem that in many Euglenineae the grains are built up from soluble substances apart from the chloroplasts[2]. Whilst they undoubtedly increase in size or number during active photosynthesis and decrease during starvation, especially the larger characteristically shaped grains would in many cases appear to possess a rather marked degree of persistence. In several species of *Euglena* and *Trachelomonas* the chloroplasts possess a so-called "pyrenoid" which bulges prominently (fig. 173, E); such pyrenoids are either naked or provided, on one or both sides, with a sheath of paramylon having the shape of a watch-glass. Many Euglenineae also store fat-globules as a food-reserve.

The vacuolar system is complex. The periplast is invaginated at the anterior end to form a short narrow canal leading down to a large and prominent contractile vacuole (cf. fig. 173, B, E–H). Near the latter are one (e.g. *Phacus pleuronectes* Duj.) or more (e.g. *Euglena deses* Ehrenb. (cf. also fig. 173, G)) accessory vacuoles which sooner or later fuse with the main one, after which the latter gradually contracts to its original dimensions, no doubt discharging into the canal. During the gradual enlargement of an accessory vacuole a rosette-like group of minute vacuoles appears around its periphery and, as the former fuses with the main vacuole, the members of the rosette unite to form a new accessory vacuole. In many Euglenineae a prominent eye-spot is situated near the main vacuole (fig. 173, *s*).

The flagella usually arise from the canal and, in several species,

[1] cf. Schmitz, 1882, p. 155; Bütschli, Archiv f. Protistenk. VII, 1906, p. 197; Molisch, Mikrochemie, 1923, p. 390.

[2] This is evident also in the production of paramylon in the colourless forms that lack plastids.

it has been shown that they extend back to the posterior end of the main vacuole, where they are connected with a basal granule; in some *Euglenas* the flagellum forks on entering the vacuole, one of the two forks bearing the basal granule. In some cases (*E. sanguinea*), moreover, these forks appear to be prolonged into the cell, terminating in a special granule located near the nucleus[1]. The latter is usually large and prominent and exhibits a central "nucleolus" around which the chromatin is radially distributed (fig. 173, *n*). In the nuclear division of *Euglena*[2] no spindle is formed, the chromosomes grouping themselves around the drawn-out nucleolus and ultimately separating into two groups about the two halves of the latter.

In the majority of cases the individuals are naked, but in *Trachelomonas* (fig. 174, C, F) and *Ascoglena* (fig. 174, D) they are enclosed within a special envelope separated from the protoplast by a well-marked space and provided with an apical aperture for the emergence of the flagellum (cf. *Coccomonas* among Chlamydomonadales, *Chrysococcus* among Chrysomonadales). In *Trachelomonas* the individuals are free-swimming, but in *Ascoglena* the soft and wide envelope is attached to filamentous Algae. A similar epiphytic habit is seen in *Colacium* (fig. 174, A), where the motionless individuals are situated at the end of a simple or branched system of mucilage-stalks; a flagellum is only acquired in connection with reproduction.

A considerable number of the genera of Euglenineae are permanently colourless (*Astasia*, *Peranema*), such forms being altogether devoid of plastids and leading a saprophytic existence; in *Peranema* and its allies holozoic nutrition is effected with the help of a special rod-shaped organ, acting as a kind of suction-pump and located at the anterior end of the individual. Colourless forms are also known in the genus *Euglena*[3]. *E. gracilis* Klebs, when grown in culture-solutions in the dark, becomes colourless, although retaining its plastids; on exposure to light the latter again become green. It has been shown, however, that in cultures individuals of this species can arise that lack plastids and are therefore permanently colourless; Ternetz suggests that this is due to one of the chloroplasts of a given individual losing the faculty of division, so that after a certain number of generations some of the offspring would be colourless[4]. *Euglena*

[1] cf. Wager, Journ. Linn. Soc. Zool. XXVII, 1900, p. 472; Haase, Archiv f. Protistenk. XX, 1910, p. 49.

[2] cf. Tschenzoff, Archiv f. Protistenkunde, XXXVI, 1916, p. 137, where earlier references are given.

[3] cf. Zumstein, Jahrb. wiss. Bot. XXXIV, 1900, p. 184; Ternetz, ibid. LI, 1912, p. 435.

[4] Ternetz, loc. cit. p. 496.

quartana Moroff and *Trachelomonas reticulata* Klebs are permanently colourless and devoid of plastids.

Reproduction is as usual effected mainly by longitudinal division. In most Euglenineae the individuals come to rest, secrete an envelope of mucilage, and then proceed to divide, fission commencing at the front end of the protoplast. In certain forms (e.g. *Euglena*) the cells tend to round off at these times and may divide again and again to form palmelloid groups, easily distinguished from the similar stages found in other classes by the presence of paramylon. Thick-walled cysts are often formed in the species of *Euglena*. An isogamous sexual process, involving the fusion of amoeboid gametes, has been recorded by Haase (loc. cit. p. 52) for *Euglena sanguinea* Ehrenb., but this requires confirmation. Dobell[1] has described a fusion of ordinary individuals, accompanied by nuclear division and abortion of one of the two resulting nuclei of each gamete, in *Scytomonas pusilla* Stein (*Copromonas subtilis* Dobell), a saprophyte in the alimentary canal of the frog.

Lemmermann[2] is responsible for the most recent systematic treatment of the Euglenineae which are classed in three families, viz.:

1. *Euglenaceae*, mostly with radial organisation, usually with chloroplasts, and division generally in the resting condition.
2. *Astasiaceae*, with radial organisation, no plastids, and division in the motile phase.
3. *Peranemaceae* with dorsiventral organisation, no plastids, and often showing holozoic nutrition.

In conformity with the scope of this book, only the pigmented Euglenaceae are dealt with below. The British genera can be determined with the help of the following key:

A. Individuals free-swimming, not epiphytic
  a. With a single flagellum
    1. Naked, without a special envelope
      * Cells often metabolic, often elongate, paramylon-grains showing diverse shape and arrangement — *Euglena*
      ** Cells with a rigid periplast, large paramylon-grains
        † Cells not flattened, usually with two lateral ring-shaped paramylon-grains — *Lepocinclis*
        †† Cells markedly flattened — *Phacus*
    2. Cells with a firm, usually brown-coloured envelope[3] — *Trachelomonas*
  b. With two flagella — *Eutreptia*

[1] Quart. Journ. Microscop. Sci. LII, 1908, p. 75.

[2] Lemmermann, 1910, p. 484; Lemmermann, in Pascher, 1913, p. 115; see also Klebs, Unters. Bot. Inst. Tübingen, I, 1883, p. 236.

[3] cf. *Chrysococcus*, p. 322.

B. Individuals epiphytic, sometimes colonial
  a. Individuals solitary, with a wide relatively soft envelope *Ascoglena*
  b. Individuals on simple or branched mucilage-stalks, naked *Colacium*

Euglena Ehrenberg, 1838[1]. Motile, with a short or very elongate flagellum, and a soft or more or less rigid, rather coarse periplast which is often longitudinally or spirally striated (sometimes with lines of small warts), often markedly metabolic; cells commonly elongate-lanceolate or spindle-shaped, sometimes spirally twisted and occasionally produced into a colourless tip at the posterior end. Chloropl. usually numerous and discoid, but band-shaped in some sp. and then often aggregated to form one, two, or more stellate groups (or single star-shaped chloropl.? (cf. fig. 1, H)); "pyrenoids" occasionally present, naked or with a paramylon-sheath; paramylon-grains few or many, in the former case often only two ring- or rod-shaped ones, the one anterior, the other posterior (fig. 173, B, F), in the latter case of diverse form (rods, ovoid bodies, discs, etc.); eye-spot mostly present. Accessory contr. vacs. one or several. Reprod. by longit. div. of individuals, usually enveloped in mucilage. Cysts with a thick stratified membrane. Sex. reprod. by fusion of amoeboid isogamous gametes recorded in *E. sanguinea* Ehrenb. (cf. p. 410).

Sp. of *Euglena* are exceedingly common in small stagnant ponds, especially such as are rich in organic matter (e.g. farmyard ditches). The irregular cycles often follow immediately on the periodical dying away of the filamentous Algae and other aquatics (cf. Fritsch and Rich, 1913, p. 52). In some cases the individuals constitute a green film on the surface of the water, while the resting-stages often form a conspicuous red coating on the surface of drying mud.

Eight Brit. sp. have been recorded, but many others certainly occur. One of the commonest is *E. viridis* Ehrenb. (fig. 1, H), with a single stellate group of band-shaped chloropl. and a delicate striated periplast; the cells are highly metabolic, 52–57 l. Three large and striking sp., that exhibit little metaboly, are *E. oxyuris* Schmarda, *E. tripteris* (Duj.) Klebs, and *E. spirogyra* Ehrenb. (fig. 173, F). The first two are always spirally twisted and the same feature may be shown by the last; all three exhibit prominent striation of the periplast, which is longit. in *E. tripteris* and spiral in the two others; *E. tripteris* has two large rod-shaped paramylon-grains, whilst in the others there are two ring-shaped ones. Rod-shaped paramylon-

[1] cf. Wager, Dellinger, Hamburger, and Haase, loc. cit.; Schmitz, Jahrb. Wiss. Bot. xv, 1884, p. 2; Klebs, loc. cit. p. 297; Dangeard, Le Botaniste, viii, 1901, p. 132; Naumann, Skrift. Södra Sverig. Fiskerifören. No. 12, 1914; van Oye, Bull. Soc. Roy. Bot. Belgique, lvi, 1924, p. 124; Deflandre, Rev. Algol. i, 1924, p. 235.

grains are also seen in *E. acus* Ehrenb. (fig. 173, A, B) which is characterised by its narrow spindle-like form (140–180 l.), with delicate

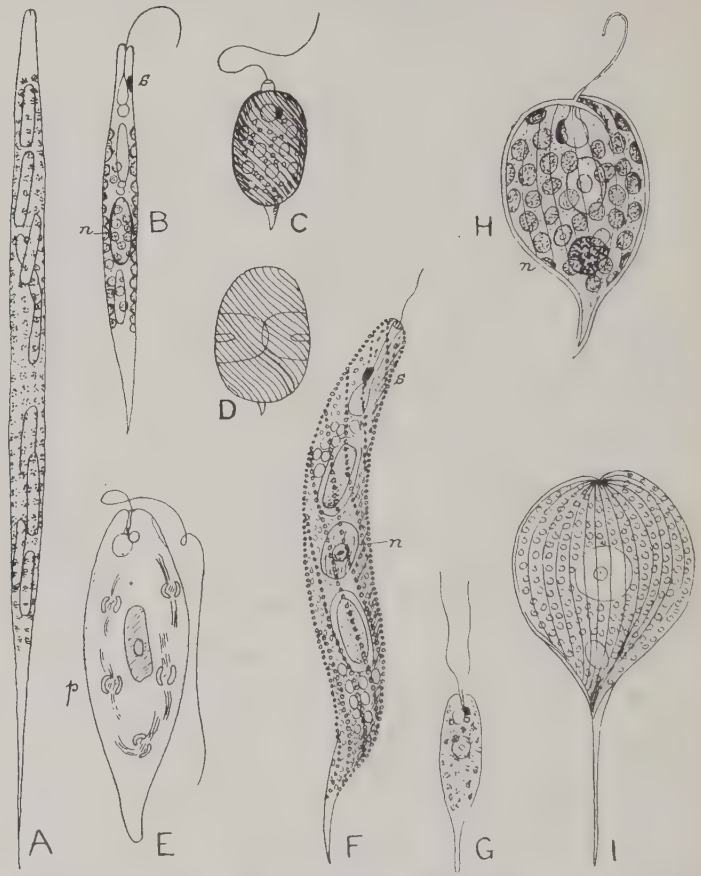

Fig. 173. A–B, *Euglena acus* Ehrenb.; A, after Deflandre, ×375; B, after Klebs, ×300. C–D, *Lepocinclis ovum* (Ehrenb.) Lemm.; C, after Stein, ×490; D, form, showing the two large lateral paramylon-grains (after Fritsch, ×600). E, *Euglena polymorpha* Dang. (after Dangeard, ×525). F, *E. spirogyra* Ehrenb. (after Lemmermann, ×325). G, *Eutreptia viridis* Perty (after Lemmermann, ×200). H, *Phacus pleuronectes* (O. F. M.) Duj. (after Senn, from Engler-Prantl, Natürl. Pflanzenfam. ×750). I, *P. longicauda* (Ehrenb.) Duj. (after Lemmermann, ×590). *n*, nucleus; *p*, pyrenoid; *s*, stigma.

spiral striation of the periplast. In *E. sanguinea* Ehrenb. the individuals are coloured red by haematochrome. The resting-stages exhibit a similar colour in several other sp.

Lepocinclis Perty, 1852[1]. Motile, with a more or less elongate flagellum and a rigid usually spirally striated periplast, not metabolic; cells circular in cross-section, in general shape ovoid, elliptical, or lanceolate-elliptical, often with a straight pointed posterior spine. Chloropl. numerous, discoid, parietal; paramylon-grains usually two, large and ring-shaped, laterally disposed (fig. 173, D); "pyrenoids" absent; eye-spot occasionally present. Reprod. by div. as in *Euglena*. Resting-stages like the ordinary individuals, but devoid of the flagellum.

The genus is closely allied to *Euglena*. The sp. are found in the same habitats as those of the latter, although often favouring rather cleaner water; they are widely distributed, but usually occur in small numbers. Of the three Brit. sp., *L. ovum* (Ehrenb.) Lemm. (fig. 173, C, D; 30–38 l.) is the commonest. *L. Steinii* Lemm. differs in the possession of short spindle-shaped cells (22–30 l.) and the almost longit. striation of the periplast.

Phacus Dujardin, 1841[2]. Motile, with a short or elongate flagellum and a rigid, usually longit. or spirally striated periplast, the striations sometimes bearing spines or warts, not metabolic; cells mostly prominently flattened, often with one surface slightly convex and the other slightly concave, the flat faces roughly oval or elliptical in outline, the posterior end usually pointed and often prolonged into a short or long spine which is sometimes turned to one side; cells occasionally twisted, the periplast in some sp. with a fold or keel running more or less longit. over part or over the whole of the convex (dorsal) surface. Chloropl. numerous, discoid, parietal; sometimes one or two large paramylon-grains, sometimes numerous small rounded or elongate grains, occasionally none; "pyrenoids" absent; eye-spot rare. Reprod. as in *Lepocinclis*; resting-stages little known, with a thick mucilage-envelope.

About ten Brit. sp. are known and several of them are common in the habitats frequented by *Euglena* and *Lepocinclis*. Such are *P. pleuronectes* (O. F. M.) Duj. (45–48 l.) (fig. 173, H) with a fold on the convex side extending to the middle of the cell, *P. longicauda* (Ehrenb.) Duj. (80–115 l.) (fig. 173, I), and *P. caudata* Hübner (45 l.) with the fold extending the whole length of the convex surface; all three have one or two large ring-shaped paramylon-grains, whilst the first and last have a slightly twisted body. Most of the other sp. seem to be very local. Of *P. pleuronectes* a colourless var. *hyalina* is known which sometimes occurs in enormous quantities in old cultures.

[1] Lemmermann, Ber. Deutsch. Bot. Ges. XIX, 1901, p. 87; Fritsch, 1914, p. 349.

[2] Dangeard, loc. cit. p. 203.

Trachelomonas Ehrenberg, 1833[1]. Motile, with a usually elongate flagellum and a delicate unsculptured periplast, highly metabolic, the protoplast loosely encased in a spherical, ovoid, oblong, or otherwise shaped, rigid envelope, from which it may at times escape; the envelope smooth, granulate, spiny, hispid, etc., at first hyaline, later generally coloured yellow, brown, or dark brown by iron salts and then more or less obscuring the protoplast, the flagellum emerging at the anterior end through a wide circular aperture, the rim of which is often thickened or produced as a cylindrical collar. Chloropl. two curved plates or numerous discs; paramylon present or absent, in the form of small grains; "pyrenoids" often present; eye-spot frequent. Reprod. by longit. or transv.[2] div., one daughter-individual

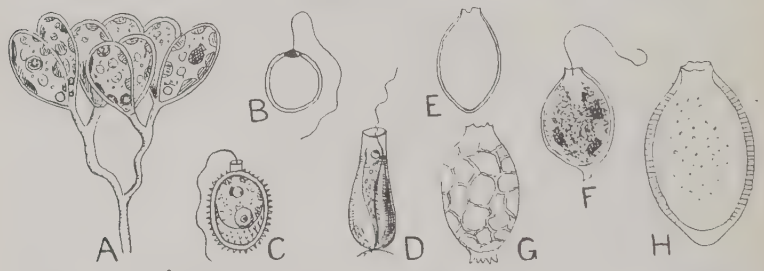

Fig. 174. A, *Colacium arbuscula* Stein (after Stein, ×490). B, *Trachelomonas volvocina* Ehrenb. (after Lemmermann, ×420). C, *T. hispida* (Perty) Stein (after Lemmermann, ×355). D, *Ascoglena vaginicola* Stein (after Lemmermann, ×325). E–H, *Trachelomonas inconstans* Carter (after Carter, E–G, ×390; H, ×600); F, living individual; H, shows structure of envelope.

retaining the envelope and flagellum of the parent, whilst the other forms a new flagellum, escapes through the flagellar aperture, and gradually secretes a new envelope. Resting-stages like the ordinary individuals, but devoid of a flagellum.

The protoplast in most sp. of this genus is very imperfectly known, specific distinction being based almost entirely on the form and other characters of the envelope. Six sp. are recorded for the Brit. Isles. Of these, *T. volvocina* Ehrenb. (fig. 174, B), with a smooth spherical envelope (7–21 br.), and *T. hispida* (Perty) Stein (fig. 174, C), with an oval envelope covered with numerous fine spines (20–42 l.; 15–26 br.), are very widespread and often occur in large numbers in stagnant pools; a number of varieties of each sp. is known. *T. oblonga* Lemm., with a smooth oblong envelope (13–16 l.), is rarer. In *T. rugulosa*

[1] Dangeard, loc. cit. p. 223; Conrad, Annales Biol. lacustre, VIII, 1916, p. 193; Carter, New Phytol. XVIII, 1919, p. 118; Skvortzow, Biol. Sungari Stat. Harbin, I, 1925, Heft 2.

[2] cf. Lemmermann, 1910, p. 519.

Stein the spherical envelope (15–23 br.) is provided with spiral ridges (fig. 2, B, p. 29).

Eutreptia Perty, 1852[1]. Motile, with two flagella of the length of the cell and a rather soft striated periplast, highly metabolic; cells more or less spindle-shaped, attenuated or produced into a narrow process at the posterior end. Chloropl. numerous, discoid: paramylon-grains spherical, shortly cylindrical, etc.; "pyrenoids" absent; eye-spot present. Reprod. by div., as in *Euglena*, or in the motile condition. Cysts with a thick stratified membrane.

So far there is only one record of *E. viridis* Perty (fig. 173, G), from Staffordshire (cf. Grove, 1920, p. 4); cells 49–66 l. and 5–13 br.

Ascoglena Stein, 1878[2]. Epiphytic, solitary; cells fusiform or broadly ovoid, with a distinct but soft periplast, metabolic, attached by their posterior end to the base of a cylindrical or urn-shaped roomy envelope which is of soft texture, yellow or brown in colour in older individuals, and provided with a wide aperture through which the single flagellum projects. Chloropl. numerous, discoid, with or without "pyrenoids" having a paramylon-sheath; eye-spot present. Reprod. as in *Trachelomonas*, the one daughter-individual after a swarming period attaching itself to a substratum by its posterior end and secreting an envelope, which is at first very delicate and mucilaginous. No resting-stages known.

Delf[3] records an unnamed sp. of this genus attached to various filamentous Algae in ponds on Hampstead Heath. *A. vaginicola* Stein (fig. 174, D) is a sp. that has often been recorded on the continent.

Colacium Ehrenberg, 1838[4]. Epiphytic on plankton-organisms (esp. Copepods), usually colonial, individuals devoid of flagella, situated at the ends of simple or branched mucilage-stalks; cells with a thin mucilage-envelope, ovoid, spindle-shaped, or cylindrical. Chloropl. numerous, discoid, with "pyrenoids" having a paramylon-sheath. Multipl. of cells by longit. div.; reprod. by swarmers (with a single flagellum and an eye-spot) which become attached by their front end and secrete a mucilage-stalk. No resting-stages known.

C. arbuscula Stein (fig. 174, A) has been found epiphytic on free-swimming Rotifers in the Birmingham district.

[1] Klebs, loc. cit. p. 315.
[2] Klebs, loc. cit. p. 316.
[3] New Phytol. XIV, 1915, p. 68.
[4] Dangeard, loc. cit. p. 199; Klebs, loc. cit. p. 321.

CLASS X. RHODOPHYCEAE[1]

This large class is almost entirely confined to the sea, the few freshwater representatives being in the main characteristic members of the algal flora of streams and rapids. The Rhodophyceae are distinguished by a complete absence[2] of motile reproductive units, both the asexual cells (monospores and tetraspores) and the male cells (spermatia) being devoid of cilia, though apparently often endowed with some slight capacity for amoeboid movement. A possible flagellate origin is therefore merged in complete obscurity, the more so as practically all the known representatives of the class are typical and often highly differentiated filamentous or parenchymatous "algal" forms. It is probably at the present time quite futile to speculate as to the origin and affinities of this very sharply circumscribed class, and the attempts to relate the somewhat aberrant Bangiales to forms such as *Prasiola*[3] or the Myxophyceae appear altogether rash in the present state of our knowledge.

The Rhodophyceae exhibit a variety of colours from bright red and purple to dark brownish-reds, brownish-green, blue-green, and black. The colour is due to special pigments which are present in the chromatophores side by side with the ordinary green and yellow ones. In the majority of cases the pigment concerned is the water-soluble *phycoerythrin*, which has been obtained in crystalline form and is of the nature of a protein. In a number of cases, however, a second pigment, *phycocyanin*[4], exhibiting different shades of blue, occurs as well, and it is the varying combination of phycoerythrin, phycocyanin, and the ordinary pigments that conditions the diverse shades of colour, both in the different species and in the same species at different seasons. Possibly the species of *Batrachospermum* lack phycoerythrin altogether, their colour being due to admixture of phycocyanin with the ordinary chloroplast-pigments.

The chromatophores themselves are very varied—band-

[1] Of the ninth class, the Phaeophyceae, no freshwater representatives are known to occur in Great Britain.

[2] Yendo's record (Bot. Mag. Tokyo, xxxiii, 1919, p. 91) of the occurrence of motile micro- and macro-gametes in the Bangiales has been disputed by other Japanese workers (cf. ibid. xxxiv, 1920, p. 131) and cannot be accepted until fully confirmed.

[3] cf. Lagerheim, Ber. Deutsch. Bot. Ges. x, 1892, p. 372.

[4] cf. Kylin, Zeitschr. f. physiol. Chem. lxxvi, 1912, p. 396, and Svensk. Bot. Tidsskr. vi, 1912, p. 533.

shaped, stellate, irregularly lobed bodies, or numerous small discs. The Bangiales are characterised by a single axile stellate chromatophore in each cell (cf. fig. 181); the central part is occupied by a large pyrenoid and the numerous rays often broaden out in the parietal cytoplasm. In the Rhodophyceae proper (Florideae) the chromatophores are generally parietal and two or many in number. Pyrenoids seem to be of frequent occurrence in the Nemalionales, but very rare in the higher Florideae. The characteristic assimilatory product is a polysaccharide, the so-called *Floridean starch*[1], which appears in the form of small doubly refractive granules staining brownish or reddish with iodine. The grains sometimes accumulate in the neighbourhood of the pyrenoids without, however, usually forming a definite shell.

The cells of the Red Algae commonly contain more than one nucleus when mature. In a large number of cases the relatively thick mucilaginous walls separating adjacent cells are provided with large pits (cf. fig. 176, D), occupied by broad protoplasmic strands connected by delicate cytoplasmic threads traversing the thin pit-membrane. The exact composition of the cell-wall is not adequately known in any case.

The vegetative body is rarely built up of a simple unbranched (*Bangia* (fig. 181, F)) or branched filament (*Chantransia* (fig. 176), *Callithamnion*). More commonly the thallus is composed of an axis comprising a single row of large cells (*Batrachospermum* (fig. 177)) or a series of parallel or interwoven longitudinal filaments (*Thorea* (fig. 179, A); *Nemalion*), from either of which arise numerous closely set whorls of richly branched laterals which may be so dense as to give rise to a more or less firm cylindrical structure (*Thorea*, *Nemalion*). In *Lemanea* (figs. 175, D; 178) the laterals are fitted together to form a compact parenchymatous cortex. A somewhat different construction is seen in *Compsopogon* (fig. 179, C, D), where, much as in the marine *Ceramium*, a central axis of large cells is enveloped by a small-celled cortex. Other types are exemplified by the 1- or 2-layered flat expanses of *Porphyra* and the crusts of *Hildenbrandtia*, which are composed of compactly arranged vertical filaments (fig. 180). These few statements are only indicative of the complex organisation of many Florideae, a detailed consideration of which (apart from that of the freshwater genera given below) is beyond the scope of this book. Growth in the filamentous types is mainly apical.

[1] cf. Schmitz, 1882, p. 151; Bütschli, Verh. d. Nat.-Med. Ver. Heidelberg, VII, 1903, p. 519; Kolkwitz, Wiss. Meeresunters., Abt. Helgoland, IV, 1900, p. 33; Molisch, Mikrochemie, 1923, p. 388.

Sharply characterised as the Red Algae are by the pigmentation of the chromatophores and the nature of the assimilatory product, it is the reproductive processes that give their special stamp to the class. In a few genera (*Lemanea*, *Nemalion*) the only method of reproduction known is a sexual one, but in most cases there is also asexual reproduction of a distinctive type. The sporangia in which the spores arise are swollen, usually spherical, structures containing a protoplast with bright red or otherwise coloured chromatophores and an abundance of reserve-substances; the contents are liberated, after rupture of the membrane, as a single naked *monospore* (Bangiales, Nemalionales, cf. fig. 176, B) or four naked *tetraspores* (the remaining Florideae); both kinds of spores are motionless and germinate direct to form a new thallus. In the higher Florideae the first nuclear division in the tetrasporangium is a reducing division[1], and as a general rule the tetraspores are borne on other individuals than those bearing the sexual organs.

The latter comprise antheridia and carpogonia, which are commonly found on distinct plants. The *antheridia* (fig. 175, C, *a*) are small rounded colourless cells which, in the loosely branched types, are situated in small groups at the extremities of the lateral branches (*Batrachosperum*), although in the more compact (marine) forms they are often embedded in the tissue of the thallus. Each antheridium produces a single colourless naked male cell or *spermatium*[2]. The female organ or *carpogonium* (figs. 175, B; 177, F) usually terminates a short branch and is commonly flask-shaped, being produced at its upper end into a more or less elongate process, the *trichogyne* (*t*), which serves as a receptive organ. The nucleus, chromatophores, and reserve-substances are located in the lower swollen part, whilst the trichogyne contains only colourless cytoplasm; prior to fertilisation the nucleus divides, one part passing into the trichogyne. There is no contraction of the contents of the carpogonium to form a definite female cell[3].

The spermatia have approximately the specific gravity of the water into which they are shed and can float for some considerable time. Their large numbers ensure contact with a trichogyne the tip of which is evidently more or less mucilaginous. At this stage the spermatium has acquired a delicate wall and, soon after,

[1] cf. for instance Lewis, Ann. of Bot. XXIII, 1909, p. 663.

[2] In *Batrachospermum* there are traces of chromatophores in the spermatium.

[3] cf. Davis, Ann. of Bot. X, 1896, p. 49; Schmidle, Bot. Zeit. LVII, 1899, p. 125; Osterhout, Flora, LXXXVII, 1900, p. 109; Kylin, Ber. Deutsch. Bot. Ges. XXXV, 1917, p. 155.

the membranes at the point of contact are dissolved, so that an open communication is established between the contents of spermatium and trichogyne (figs. 175, A; 177, F). In *Batrachospermum* and *Nemalion* the nucleus of the spermatium undergoes division, but this is apparently exceptional. In any case only

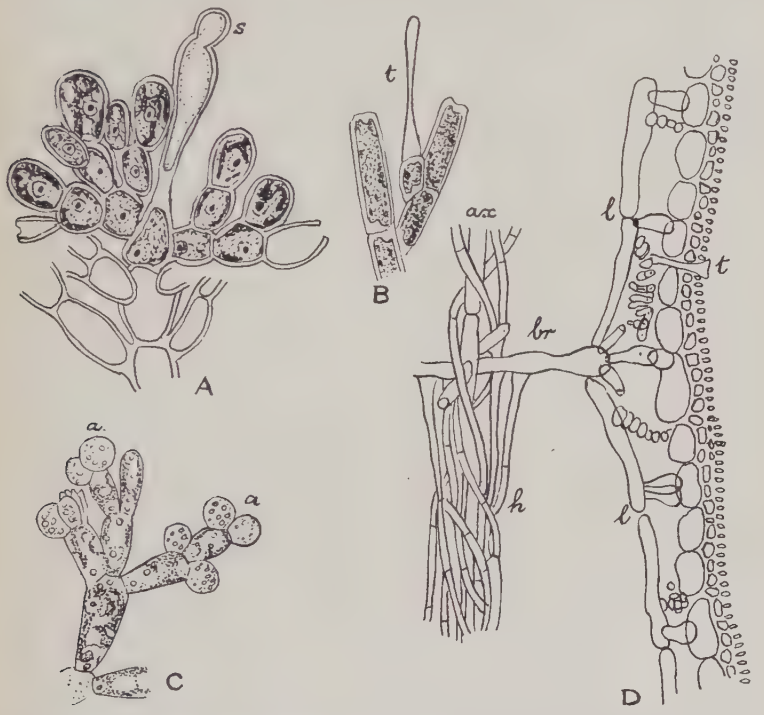

Fig. 175. A, *Batrachospermum moniliforme* Roth, fertilised carpogonium showing development of sporogenous threads (after Kylin, ×850); *s*, spermatium. B, *Chantransia corymbifera* Thuret, carpogonium (after Thuret, ×400); *t*, trichogyne. C, *Batrachospermum moniliforme* Roth, branch with antheridia (*a*) (after Sirodot, × 800). D, *Lemanea australis* Atkins. (after Atkinson, from Oltmanns), longitudinal section of part of one of the bristle-like thalli; *ax*, axial thread; *br*, one of the four laterals arising from the axial thread; *h*, "hyphae"; *l*, longitudinal threads (see p. 426); *t*, trichogyne.

one spermatium nucleus passes down to the base of the carpogonium to fuse with the female nucleus. The trichogyne then becomes separated off by a plug of mucilage (fig. 175, A) and sooner or later shrivels up.

Soon after fusion the nucleus of the zygote divides and one half passes into a lateral protrusion of the carpogonium which is

thereupon cut off by a separating wall; the other daughter-nucleus divides again and the same events are repeated. In this way a whole series of cells are formed around the periphery of the carpogonium. These, in most Nemalionales (*Batrachospermum*, *Lemanea*), grow out into short *sporogenous threads* (*gonimoblasts*, cf. fig. 175, A), the terminal cell, or several cells, of which swell up to form *carposporangia* with a dense deeply coloured protoplast. The contents of each such cell are liberated as a single naked *carpospore* which germinates immediately to form a new individual. It has been shown for several Nemalionales that the first nuclear division of the zygote is a reduction division. The life-cycle of these forms is thus analogous to that of *Coleochaete* (cf. p. 180) and, looked at purely from the cytological point of view, the sporophyte is represented solely by the zygote, whilst the gametophyte occurs in two phases, the sporogenous threads producing carpospores and the ordinary individual producing monospores and sexual organs[1].

In the higher Florideae (which are almost entirely marine), however, the life-cycle is more complex. One or more cells are cut off from the fertilised carpogonium and these fuse with adjacent cells of the thallus (*auxiliary cells*) which are either located in the immediate neighbourhood of the carpogonium (*Callithamnion*, *Ceramium*) or at some distance away from it; in the latter case the cells cut off from the carpogonium develop into long septate threads which grow towards the auxiliary cells, probably under the influence of a chemotropic stimulus (*Dudresnaya*). Fusion with the auxiliary cells is purely cytoplasmic, the nuclei involved remaining quite independent of one another, but the ultimate result of each such fusion is the production of a group of carposporangia producing carpospores similar to those of the Nemalionales. In the Florideae showing these features there is no reduction of chromosome-number when the zygote-nucleus divides and the resulting carpospores are diploid, not haploid as in the Nemalionales. They give rise to a diploid thallus bearing tetraspores and, as above stated, it is during the formation of these that reduction takes place. The tetraspores then give rise to a haploid thallus bearing sexual organs. This elaborate alternation is thus of a different type from that met with in the Nemalionales[2].

In many of the higher Florideae the effects of fertilisation are not confined to the carpogonium, outgrowths arising from the underlying cells of the carpogonial branch and forming an investment around the carposporangial threads.

[1] cf. Cleland, Ann. of Bot. xxxiii, 1919, p. 323.

[2] See Svedelius, Ber. Deutsch. Bot. Ges. xxxix, 1921, p. 178; Fritsch, New Phytol. xv, 1916, p. 247; Oltmanns, Morph. u. Biol. d. Algen, ii, 1922, p. 431.

The Red Algae are usually divided into:

I. *Bangiales* (*Bangia*, *Porphyra*), with a thallus of simple structure without pits between the cells and with an axile stellate chromatophore in each cell; reproduction by monospores and sexually, the female organs simpler than those of the Florideae, the spermatia very similar. The relation of this group to the Florideae is not at all clear and there is possibly no close affinity. Its few members are marine, except for *Porphyridium* (fig. 181, E, cf. p. 430), now usually regarded as a reduced member of the Bangiales, and *Bangia atropurpurea* (Roth) Ag. (fig. 181, F) which is found in the estuaries of some British rivers. The latter appears in the form of unbranched basally attached filaments, at first consisting of a single row of cells which later become divided up by a large number of variously orientated walls.

The genera *Asterocystis* (fig. 181, B D) and *Chroothece* (fig. 181, A), which have been regarded as members of the Myxophyceae by many systematists, have recently[1] been classed among the Bangiales by Pascher. They would certainly seem to have little in common with the bulk of the Blue-green Algae, but are so incompletely known that one is loth to assign an exact position among the Rhodophyceae to them. Like *Porphyridium* they are here treated at the conclusion of the consideration of the freshwater Florideae[2].

II. *Florideae*, comprising the main mass of the Red Algae and to which the bulk of the previous descriptive matter applies. They are usually classed in the four series Nemalionales, Gigartinales, Rhodymeniales, and Cryptonemiales, which are distinguished by the events following fertilisation and the mode of production of the carpospores. All the known British freshwater forms belong to the Nemalionales, with the exception of *Hildenbrandtia* whose position is very uncertain; it is usually placed in the Cryptonemiales and is regarded by some as a non-encrusted member of the Corallinaceae (cf. p. 430).

The following is an artificial key for the determination of the few British freshwater genera of Rhodophyceae, including the reduced forms above referred to:

A. Chromatophores various, but not stellate; cells connected by protoplasmic strands

[1] Pascher, 1925, p. 138. In Engler and Prantl's "Natürliche Pflanzenfamilien" (1 Teil, Abt. II, p. 314) *Asterocystis* is treated as a doubtful genus of the Bangiales, whilst Kirchner (Pflanzenfam. 1 Teil, Abt. 1 *a*, p. 54) advocates a reference of *Chroothece* to the same group; cf. however West, 1916 *a*, p. 39.

[2] The writer, while not convinced of the relationship, is in no way in favour of these genera being retained among the Blue-green Algae.

a. Thallus composed of simple branched filaments
1. Filaments irregularly branched, older cells not usually invested by special cortical threads *Chantransia*
2. Filaments with dense whorls of lateral branches, appearing like beads of a necklace to the naked eye, older cells overgrown by cortical threads *Batrachospermum*
3. Filaments richly, but irregularly branched, the large cells of the older portions being covered by a 1-layered parenchymatous cortex *Compsopogon*

b. Thallus composed of coarse unbranched or branched cylindrical threads showing a pseudoparenchymatous structure
1. Thallus usually unbranched, bristle-like, with nodose swellings, reaching a length of 15–18 cms. *Lemanea*
2. Thallus branched, soft, without swellings, densely clothed with hairs, 30–60 cms. long *Thorea*

c. Encrusting aquatic form attached to stones, thallus composed of closely apposed vertical filaments *Hildenbrandtia*

B. Chromatophores stellate, with a central pyrenoid, cells embedded in mucilage, not connected by protoplasmic strands

a. Thallus filamentous, irregularly branched, blue or olive-green in colour *Asterocystis*

b. Encrusting, terrestrial, composed of several layers of globose cells embedded in mucilage *Porphyridium*

c. Cells singly or in pairs enveloped by mucilage, which forms a kind of stalk, on damp mud or rocks *Chroothece*

Of these *Chantransia* and *Batrachospermum*, with several purely marine genera, belong to the family Helminthocladiaceae, *Lemanea* to the Lemaneaceae, whilst *Thorea*, *Compsopogon*, and *Hildenbrandtia* are best regarded as *genera incertae sedis*, although undoubted Florideae. It is deemed most suitable to consider the genera alone here, without reference to the families to which they belong.

Chantransia Fries, 1825[1]. Freshwater and marine, the freshw. sp. forming dense tufts varying from about 3 to 7 mm. in height, of all shades of red, purple, and blue, not mucilaginous. Thallus composed of a branched, creeping, sometimes parenchymatous, base, giving rise to an extensive projecting filamentous system, the numerous branches of which arise from the upper end of the parent-cell and are frequently much attenuated and almost piliferous. Chromats. several, discoid or oblong, pyrens. inconspicuous (or wanting?); cell-wall moderately thin, with marked pits in the septa. Asex. reprod. by monospores formed singly in oblong sporangia which are the terminal cells of short lateral branches; some sp. with tetraspores. Sex.

[1] Brand, Hedwigia, xxxvi, 1897, p. 300; and xlix, 1909, p. 107.

organs[1] on different individuals; antheridia in clusters at the ends of short branches; carpogonia singly, in a similar position, with a long trichogyne (fig. 175, B). The fertilised carpogonium puts forth numerous short sporogenous threads, the end-cells of which develop the carpospores.

The carpospores of *Batrachospermum* and *Lemanea* develop a protonema-like growth which bears a great resemblance to *Chantransia*, and many of these growths have been described as sp. of the latter genus. These *Chantransia*-stages, which reproduce by monospores, may last indefinitely in dull light and thus the independence of most of the freshwater sp. of *Chantransia* is in question. In certain cases their relation to definite sp. of the two other genera has been indubitably established, but as such stages may in certain habitats appear year after year without giving rise to the mature form, their retention as "species" for systematic purposes is perhaps advisable.

The freshwater sp. of *Chantransia* are usually found attached to rocks and stones in rapid rivers, cataracts, and water-falls. There are some seven or eight Brit. freshwater sp., of which *C. pygmaea* Kütz. (fig. 176, A–C) and *C. violacea* Kütz. are perhaps the most frequent; the latter forms violet or reddish cushions. *C. pygmaea* is probably a stage in the life-history of *Batrachospermum moniliforme* Roth.

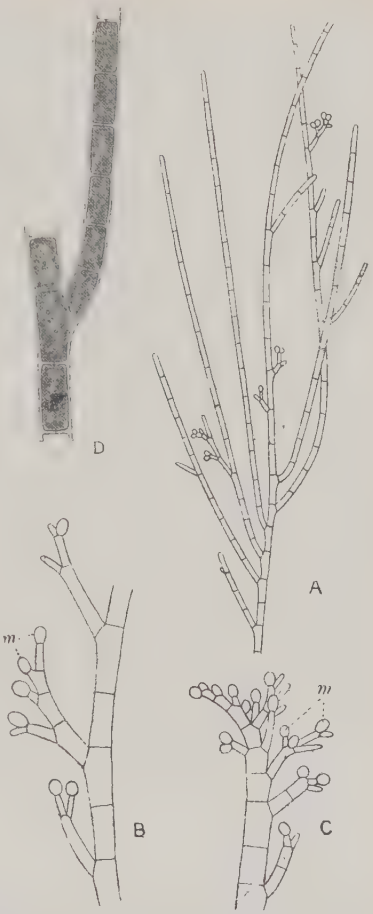

Fig. 176. A, *Chantransia pygmaea* Kütz., from Penyghent, W. Yorks (×100). B and C, branches of the same with "monospores" (*m*) (×300). D, *C. scotica* Kütz., from Cornwall; a small portion of the thallus showing the pits in the transverse walls (×400).

[1] The sexual reproduction has only been clearly recorded in *C. corymbifera* Thur., a marine sp. (cf. Bornet et Thuret, Notes Algol., Paris, 1876, p. 17).

Batrachospermum Roth, 1797[1]. Freshwater only. Thallus composed of branched bead-like threads, sometimes reaching a length of 16–20 cms., violet, violet-brown, blue-green, etc. in colour, enveloped in a thick coat of mucus. Thallus generally attached to stones or wood by a number of thick old shoots[2], which send off numerous loosely branched primary axes floating freely in the water; primary axes growing by means of a hemispherical apical cell and composed of a row of large cells which are widest at the septa (nodes), where whorls of densely branched laterals consisting of more or less moniliform cells are produced, the dense whorls of lateral branches giving the plants the characteristic beaded appearance; from the basal cells of the lateral branches cortical threads grow downward over the cells of the main axes and ultimately form a complete cortex (fig. 177, C), from which secondary (intercalary) whorls of laterals can arise; apical cells of lateral branches often produced into long hairs with a basal sheath. Chromats. parietal, lobed, with a pyren.; cells uninucleate. Asex. reprod. by monospores, usually confined to the juvenile stages (cf. below). Sex. organs on the mature thalli; antheridia spherical, in small groups at the ends of the ultimate branchlets of the whorled laterals (fig. 175, C, *a*); carpogonia singly from the lower (inner) branches of the laterals, with a clavate trichogyne (fig. 177, F). Sporogenous threads and carpospores as in *Chantransia* (fig. 175, A). Carpospores giving rise to a filamentous juvenile "*Chantransia*-stage" (cf. fig. 177, D, E) reproducing by monospores, and under suitable conditions of illumination forming several of the mature thalli which originate as lateral branches.

The sp. of *Batrachospermum* (sometimes known as the "Frog-spawn Alga") have a wide distribution in temperate and tropical climates. Most prefer deep water in which there is a slight current, more rarely they are found attached to stones in fast streams; they scarcely ever occur in stagnant water, but are found frequently in bogs, usually at a point where a spring arises. There are two more or less abundant sp. of the genus in the Brit. Islands, *B. moniliforme* Roth (fig. 177, A) and *B. vagum* (Roth) Ag. (fig. 177, B), each with a number of varieties. The latter is distinguished from the former by the more or less uniform development of the lateral branches along both the nodes and the internodes of the inferior portions of the

[1] Sirodot, Bull. soc. Bot. de France, XXII, 1875, p. 128; Sirodot, Les Batrachospermes, Paris, 1884; Brand, Bot. Centralbl. LXI, 1895, p. 280; Schmidle, loc. cit. 1899; Osterhout, loc. cit. 1900; Price, New Phytol. XIII, 1914, p. 276; Kylin, Nov. act. reg. soc. sci. Upsala, ser. 4, III, 1912, No. 3, and loc. cit. 1917.

[2] cf. West, 1904, p. 37. Other authorities do not mention these prostrate shoots.

primary axes, so that the characteristic beaded appearance is somewhat obscured. A third sp., *B. atrum* (Dillw.) Harv., with very short lateral branches and long internodes, is less widely distributed. Sp.

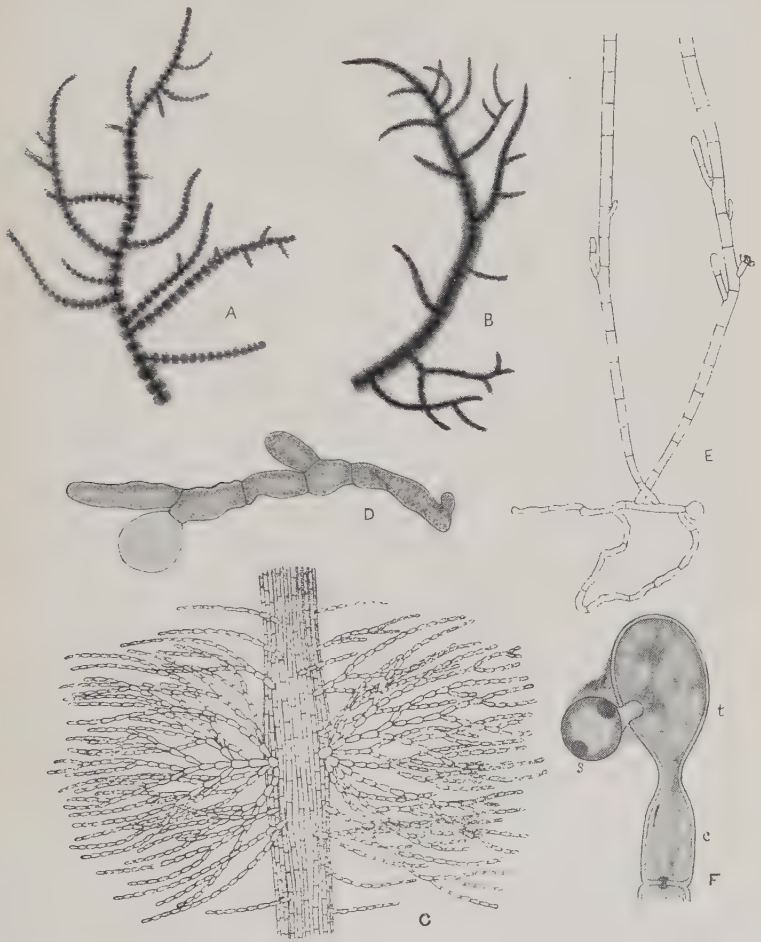

Fig. 177. A, *Batrachospermum moniliforme* Roth, from Malham Cove, W. Yorks (×2). B–C, *B. vagum* (Roth) Ag., from Thursley Common, Surrey; B (×2); C, single node with lateral branches, more highly magnified. D, germinating spore. E, juvenile stage. F, female organ and fertilisation; *s*, spermatium; *c*, carpogonium; *t*, trichogyne. (D, E, and F after Schmidle.)

of this genus commonly afford a home for epiphytes like certain sp. of *Calothrix*, *Hapalosiphon*, *Hammatoidea*, etc., and numerous Diatoms and Desmids are frequently present in the enveloping mucus[1].

[1] An excellent systematic account of the genus with abundant figures will be found in Sirodot, loc. cit. 1884, p. 199, and Pascher, 1925, p. 169.

Lemanea Bory, 1808[1] (incl. *Sacheria* Sirodot, 1872). Freshwater only, confined to rapid torrents. Thallus up to 15–18 cms. long, trailing out in the current, stiff, thread- or bristle-like, tubular, torulose (i.e. inflated at more or less equal distances), olive-green or greenish-black in colour and of a cartilaginous consistency, simple (*Lemanea*) or branched (*Sacheria*). The thallus (fig. 175, D) is built up of an axial filament (*ax*) of narrow very elongate hyaline cells, growing by means of an apical cell and giving origin just below the septa to horizontal whorls of four laterals (cf. fig. 175, D, *br*). Each of the latter consists of a large basal club-shaped cell bearing distally a number of branches, some of which pursue an almost longitudinal course (upwards and downwards parallel to the axial filament (fig. 175, D, *l*)) and produce numerous branches fitting compactly together to form a firm several-layered cortex, the outer cells of which are very small and deeply pigmented (see fig. 178, E). The swellings visible outwardly on the thallus are situated midway between the points of branching of the axial filament, which is separated from the compact cortex by a well-marked space (fig. 175, D). In the sp. of *Lemanea* proper the cells of the axial filament become surrounded by a series of twisted and slightly narrower threads ("hyphae" (fig. 175, D, *h*)) which are outgrowths from the basal cells of the laterals and fill up part of the space just mentioned. No asex. reprod. observed. Antheridia spherical, borne on short cylindrical cells, which are crowded together at the "nodes" (fig. 178, F), the antheridial areas forming either more or less complete rings (*Lemanea* (fig. 178, D)) or being situated on a number of mammilliform projections which are arranged in a verticillate manner (*Sacheria*) (fig. 178, B). Carpogonia singly, on short branches originating from the inner cortex in which the body is embedded, whilst the short simple or branched trichogyne projects slightly (figs. 175, D and 178, E, *t*). The numerous sporogenous threads grow inwards into the space around the axial filament; most of the cells swell up to form carposporangia, the carpospores being liberated on the decay of the thallus. Carpospores give rise to a *Chantransia*-stage composed of a creeping base bearing caespitose tufts of branched filaments (3–8 mm. high), from which the mature thalli arise as lateral outgrowths; the juvenile stage is relatively persistent in *Lemanea*, but fugacious in *Sacheria*.

The sp. of this genus occur attached to the rocks of water-falls, to stones and wood in mill-sluices, etc., always where the force of the water is greatest. They may be classed in two subgenera, viz. *Lemanea*

[1] Thwaites, Proc. Linn. Soc. London, I, 1849, p. 360; Sirodot, Ann. sci. nat., Bot., 5 sér. XVI, 1872, p. 5; Atkinson, Ann. of Bot. IV, 1891, p. 177; Brand, Ber. Deutsch. Bot. Ges. XIV, 1896, p. 185.

in which the thallus is usually unbranched, "hyphae" are developed around the axial filament, and the antheridial areas form more or less complete rings; and *Sacheria* in which the thallus is usually branched,

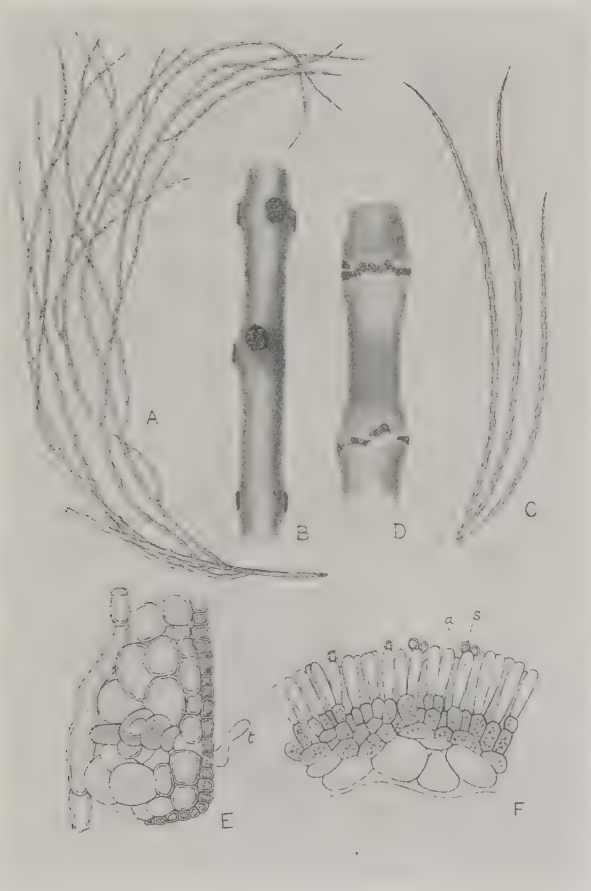

Fig. 178. A, *Lemanea* (*Sacheria*) *mammillosa* Kütz. (nat. size), from R. Wharfe, W. Yorks. B, portion slightly magnified showing antheridial areas. C, *L. torulosa* Kütz. (nat. size). D, portion slightly magnified showing antheridial areas. E, *L.* (*Sacheria*) *fucina* Bory, longitudinal section of filament showing carpogonium; *t*, trichogyne. F, *L. catenata* Kütz., transverse section of filament showing antheridial area; *a*, cylindrical cell bearing antheridia (*s*). (D, E, and F after Sirodot.)

there are no "hyphae," and the antheridial areas are on verticillate eminences. The differences do not appear sufficient to warrant generic separation, as in the first edition of this work.

Five Brit. sp. are known. *L. torulosa* Kütz. emend. Sirodot (fig. 178, C and D) and *L. parvula* Sirodot, with somewhat undulate fertile threads, belong to the subgenus *Lemanea*, but the three belonging to *Sacheria* are much more frequent. These are *L. fluviatilis* C. Ag., which is usually blackish-violet in colour[1]; *L. fucina* Bory, yellow to olive in colour; and *L. mammillosa* Kütz., which is dark green with very marked antheridial prominences (fig. 178, A–B). The last is the most abundant. It has also been found on the west side of Loch Ness, Inverness, i.e. apparently in still water, where however there are likely to be numerous currents.

Thorea Bory, 1808[2]. Freshwater only. Thallus of thin (1–1·5 mm. diam.), soft, much branched cylindrical threads, often of considerable length (30–60 cms.), purple-brown or dark brown in colour, covered with a felt of densely pigmented hairs, very mucilaginous (fig. 179, B); the bulk of the thallus is composed of irregularly intertwined hyaline threads, which near the surface assume a more longitudinal course and here bear densely arranged laterals with a number of discoid, parietal chromats. in the cells (fig. 179, A); some of these branches are very elongate and project beyond the mucilage as the above-mentioned hairs. Monospores formed within the swollen terminal cells of the shorter peripheral branches. Sex. reprod. unknown, but structures like carpogonia are recorded by Schmidle (loc. cit.). The monospores on germination give rise to a kind of *Chantransia*-stage, from which the mature plant is formed by intertwining of some of the upright threads.

This rare genus has been referred *inter alia* to the Phaeophyceae, but the pigment, the presence of starch-like granules in the cells, and the naked non-motile spores indicate a member of the Florideae. *T. ramosissima* Bory (fig. 179, A–B) has only once been recorded in Gt Britain (from Walton-on-Thames).

Compsopogon Montagne, 1850[3]. Freshwater only. Thallus richly branched, filamentous, in the mature regions rather coarse, blue-green in colour; in the upper parts the thallus consists of a single row of rather flat cells (fig. 179, C), which exhibit prolonged enlargement and multiply by transv. div.,

[1] Brand (loc. cit.) has described extensive vegetative reproduction in this sp.

[2] Möbius, Ber. Deutsch. Bot. Ges. IX, 1891, p. 333, and X, 1892, p. 266; Pfeiffer v. Wellheim, Österr. Bot. Zeitschr. XLVI, 1896, p. 315; Schmidle, Hedwigia, XXXV, 1896, p. 1; Hedgcock and Hunter, Bot. Gaz. XXVIII, 1899, p. 425.

[3] Montagne, Ann. sci. nat., Bot., sér. 3, XIV, 1850, p. 298; Schmitz, in Engler-Prantl, Natürl. Pflanzenfam., I Teil, Abt. II, p. 318; Arcangeli, Bull. soc. bot. Ital. 1898, p. 223; Thaxter, Bot. Gaz. XXIX, 1900, p. 259.

but in the older parts these divisions cease and the enlarging cells gradually cut off small superficial deeply pigmented segments, which constitute a 1-layered cortex around the large almost colourless cells of the axial series (fig. 179, D). In the

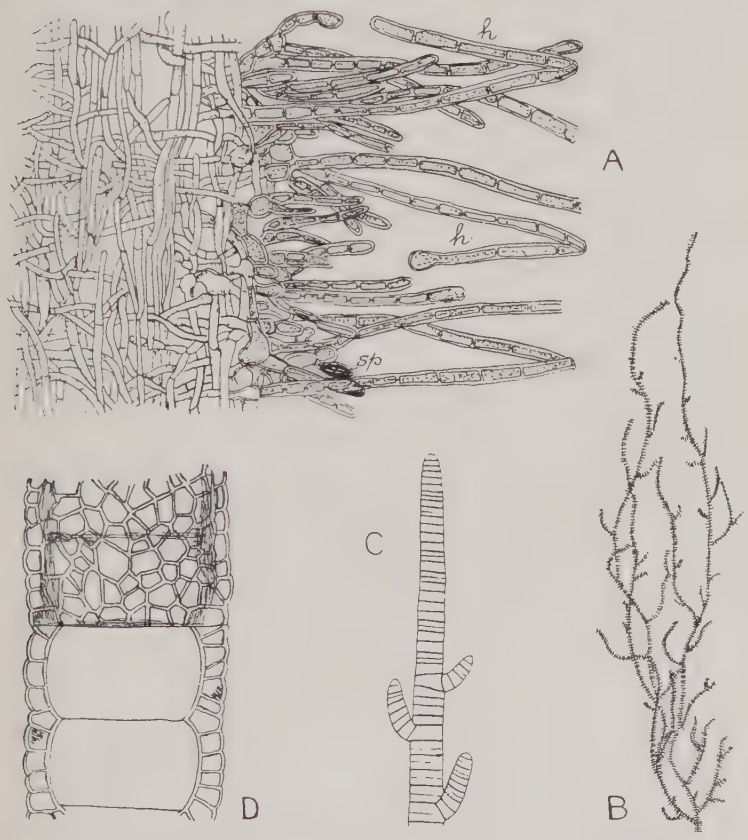

Fig. 179. A–B, *Thorea ramosissima* Bory; A, part of a longitudinal section of a thallus (after Hedgcock and Hunter, ×225); the hairs (*h*) are shown bent back upon themselves; *sp*, a cell forming a monospore; B, habit (after Schmitz, from Engler-Prantl, Natürl. Pflanzenfam., slightly reduced). C, *Compsopogon caeruleus* Mont., apex of a filament (after Schmitz, ×150). D, *C. leptoclados* Mont., part of mature filament (after Schmitz, ×150).

basal parts of the thalli this cortex is lacking, but the cells are here commonly overgrown by septate rhizoids. Branching of the threads takes place before formation of the cortex. Cells uninucleate, with numerous small parietal discoid chromats. of a bluish colour. Monospores produced in deeply pigmented cells

which are cut off from some of the cells of the cortex. Sex. reprod. unknown.

The sp. of *Compsopogon* inhabit running water and, with few exceptions, appear to be confined to tropical and subtropical regions. *C. leptoclados* Montagne (fig. 179, D) has been recorded by Weiss and Murray[1] from a part of the Reddish Canal, Manchester, where there is an influx of hot water from Cotton Mills along its banks. Like the sp. of *Pithophora* occurring in the same habitat (cf. p. 172) it is no doubt an introduction.

Hildenbrandtia Nardo, 1845[2]. Freshwater and marine. Thallus encrusting, expanded, attached by the whole of its under surface, blood-red, dark red, rose, or brown in colour, composed of compact vertically arranged filaments with small subcubical or oblong cells arising from a compact substratum. Chromat. parietal; cell-wall firm and colourless. Vegetative reprod. by detachment of parts of the thallus[3]. Asex. reprod. by tetraspores formed in rounded hollows (conceptacles) in the thallus. Sex. organs unknown.

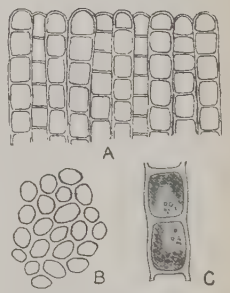

Fig. 180. *Hildenbrandtia rivularis* (Liebm.) J. Ag., from Shipley Glen, W. Yorks. A, section of thallus. B, surface view (×400). C, two cells showing the chromatophores (×800).

The only freshwater sp., *H. rivularis* (Liebm.) J. Ag. (fig. 180), occurs as dark red patches on rocks and stones in streams and dripping places; it rarely develops except in the shade and is often found on the under side of projecting rocky ledges in streams. The only method of reproduction observed is vegetative. See also p. 421.

Porphyridium Naegeli, 1849[4]. Terrestrial, forming a thin flat stratum which, when damp, is mucilaginous and blood-red in colour, when dry forms thin brittle crusts of a brownish-red or greyish-brown colour; cells reddish-purple, globose (or angular as a result of drying), in several layers, embedded in colourless homogeneous mucilage, each individual cell provided with a delicate, somewhat firmer mucilage-sheath which may

[1] Mem. Manchester Lit. and Phil. Soc. LIII, 1909, No. 14, p. 5. I am indebted to Prof. Weiss for the opportunity of examining slides of the Alga.

[2] Carter, Journ. of Bot. 1864, p. 225; Lingelsheim and Schröder, Ber. Deutsch. Bot. Ges. XXXVI, 1918, p. 271.

[3] According to unpublished observations of the writer.

[4] Naegeli, 1849, p. 71; Brand, Ber. Deutsch. Bot. Ges. XXVI *a*, 1908, pp. 413 and 540, and XXXV, 1917, p. 454; Staehelin, ibid. XXXIV, 1916, p. 893; Lewis and Zirkle, Amer. Journ. of Bot. VII, 1920, p. 333; Geitler, Rev. Algol. I, 1924, p. 362.

be developed as a kind of stalk[1]. Cell-wall thin and very elastic; chromatophores large, axile, somewhat stellate, with a large spherical central body containing the pyren, from which short lobes extend to the periphery of the protoplast; nucleus parietal, prominent. Multipl. of cells by div.; resting-stages scarcely different from the ordinary vegetative condition.

P. cruentum (Ag.) Naeg. (fig. 181, E) is a common Alga on damp ground and near the base of damp walls; the cells are 7–9 br. Widely differing opinions have been held as to its cell-structure and its

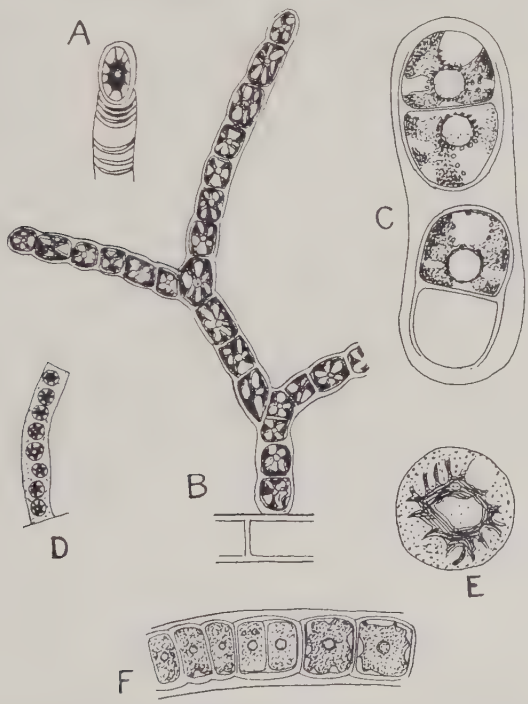

Fig. 181. A, *Chroothece Richterianum* Hansg. (after Hansgirg, ×180). B and C, *Asterocystis smaragdina* Reinsch (after Geitler); B, epiphytic on *Cladophora* sp.; C, young individual, greatly enlarged. D, *A. halophila* Hansg. (after Hansgirg, ×260). E, *Porphyridium cruentum* (Ag.) Naeg. (after Geitler), single cell, greatly enlarged. F, *Bangia atropurpurea* (Roth.) Ag. (after Schiller, ×825).

systematic position. We owe our present knowledge mainly to Brand and Geitler. Staehelin (loc. cit.) has recently again advocated its inclusion in the Myxophyceae, but neither his interpretation of the

[1] cf. Lewis and Zirkle, loc. cit. p. 335.

cell-structure, nor his conclusions have found general acceptance. Molisch[1] has shown that the pigment in the chromatophore is phycoerythrin and Brand records Floridean starch; the location of the pigment is not that customary in the Myxophyceae.

Geitler[2] has recently recorded a second sp. of the genus (*P. aeruginosum*) which is aquatic and blue-green, and is stated to have a wide distribution on the continent.

Asterocystis Gobi, 1879[3]. (*Allogonium* Kützing, 1843; *Chroodactylon* Hansgirg, 1887). Aquatic, sometimes favouring brackish water, green, blue-green, or olive-green in colour; thallus composed of spherical, ellipsoidal, or more or less quadrate cells which are embedded in a single series in simple or irregularly branched mucilage-tubes; the latter are attached to some substratum and either occur singly or form extensive strata; single cells sometimes found. About the cell-structure very diverse statements have been made. West speaks of *Asterocystis* as "a typical Chroococcaceous genus" and finds the cytology to be "similar to that of some of the larger species of *Chroococcus*,"[4] whilst Geitler describes a stellate chromatophore, blue-green in colour, with a central pyrenoid (cf. also Hansgirg, loc. cit.) and a parietal nucleus; he also records Floridean starch. It is difficult to reconcile the one account with the other, unless we assume that two totally different sets of forms are involved, some of which are actually Blue-green Algae (cf. also p. 421). Multipl. of cells by transv. div. Asex. reprod. by naked monospores recorded in one sp.

A. halophila (Hansg.) Forti (fig. 181, D) has been recorded by G. S. West (1912, p. 331) as an epiphyte on *Cladophora crispata* at Studley, Warwicks; cells 7–17 br. and 8–24 l.

Chroothece Hansgirg, 1884[5]. Cells ellipsoidal with a stout wall, singly or in pairs surrounded by a mucous envelope which, in older cells, is greatly thickened at one pole to form an elongate irregularly stratified mucilage-stalk (fig. 181, A); the cells combined to form extensive strata of various shades of orange, yellow, and green. Chromat. axile, more or less stellate, with a

[1] Sitz.-ber. Wiener Akad., Mat.-nat. Kl. CXV, 1906, p. 811.

[2] Österr. Bot. Zeitschr. LXXII, 1923, p. 84.

[3] Hansgirg, Prodr. d. Algenfl. v. Böhmen, II, Prague, 1892, p. 132; West, 1916 *a*, p. 39, footnote; Geitler, Rev. Algol. I, 1924, p. 367; Pascher, 1925, pp. 139, 159.

[4] G. S. West's drawings preserved at the British Museum (Nat. Hist.) shed no light on the cell-structure.

[5] Hansgirg, Österr. Bot. Zeitschr. XXXIV, 1884, p. 353; Ber. Deutsch. Bot. Ges. III, 1885, p. 19; and loc. cit. p. 133; West, 1916 *a*, p. 39; Wille, Nyt. Mag. f. Naturvidensk. LXII, 1924, p. 182; Pascher, 1925, p. 162.

large central pyrenoid. Multipl. of cells by transv. div. Resting cells with a thick membrane. See also p. 421.

C. Richterianum Hansg. (fig. 181, A) is known from salt marshes in Bohemia, and a small form of it (possibly another sp.) has been observed on wet limestone rocks in W. Yorks. Cells of the Brit. form 20–24 l.

Miss Acton[1] has suggested that Hansgirg's species is a member of the genus *Chroococcus*, akin to *C. macrococcus* Rabenh.

[1] Ann. of Bot. xxviii, 1914, p. 448.

CLASS XI. MYXOPHYCEAE (CYANOPHYCEAE)[1]

With the exception of a few puzzling forms, which are probably not members of this class at all[2], the Blue-green Algae are more sharply circumscribed than any other class of the pigmented Protophyta. Even the beginner, difficult as he may find generic and specific distinctions in many cases, is not long in doubt about the correct assignation of one of its members. The prevailing blue-green pigmentation, the lack of any sharp differentiation of a nucleus or a chromatophore in the cells, the abundant production of glycogen (recognised by its brown coloration with iodine) as an assimilatory product, the colonial or simple filamentous habit with copious production of mucilage often in the form of well-defined sheaths to the cells or filaments, and lastly the customary absence of any well-marked reproductive organs, all tend to give a very decided stamp to the members of this class. Both in the cell-structure and the evolution of the plant-body they stand on a relatively low plane of differentiation and, after obtaining some little familiarity with these Algae, the impression grows that one is dealing with an archaic group which has possibly remained practically unaltered during long epochs of the earth's history. Reproductive elements moving with the help of cilia are unknown[3] and no trustworthy indications of sexuality have ever been recorded. All the members of the class are "algal" in organisation and such blue-green Flagellates as have become known belong to other classes and have no relation with the Myxophyceae. An independent origin is certain, but what that origin may have been is unknown and likely to remain so. Few records of fossil Cyanophyceae exist[4], and some of these are not beyond doubt.

Perhaps one of the most interesting features of the class is its widespread occurrence and great success at the present day. Its members certainly possess a very marked power of existence

[1] The name Myxophyceae was proposed by Stizenberger (in Rabenhorst's Alg. Sachsens, 1860, p. 18) and has priority over the possibly more suitable name Cyanophyceae (Sachs, 1874).

[2] cf. *Glaucocystis* and *Gloeochaete*, p. 493; *Asterocystis* and *Chroothece*, p. 421.

[3] Goebel's (Bot. Zeit. XXXVIII, 1880, p. 490) record of zoospores in *Merismopedia* has never been confirmed.

[4] cf. Kidston and Lang, Trans. Roy. Soc. Edinburgh, LII, 1921, p. 875, and LIII, 1924, p. 612.

under adverse conditions. It would seem that many Myxophyceae can maintain themselves in almost complete darkness, when no doubt they lead a saprophytic existence[1]. They are found alike in the sea, in brackish waters, in freshwaters, and in terrestrial habitats, and often play an important rôle as plankton-organisms. The aquatic forms dominate the vegetation where other Algae (saving Diatoms) are few or absent; alike in the high temperatures of hot springs, in the frigid lakes of the Antarctic, in rushing torrents and cataracts, and in inhospitable terrestrial habitats they not only hold their own, but play a very conspicuous part. On the pebbles and boulders of streams, on the soft mud of salt-marshes, and on bare sandstone rocks, they are often the pioneers paving the way for other vegetation[2]. In moist climates many of the richest tints of the landscape are due to these Algae, and in some regions they give a decided character to the country[3]. A considerable number occur as the algal constituents of Lichens, whilst others play an appreciable rôle in the formation of calcareous or siliceous rock-masses. Further details on many of these points are given at the end of this section (p. 449).

The Blue-green Algae rarely occur as single cells (some species of *Chroococcus* and *Tetrapedia* (fig. 184, D)), more commonly the unicellular forms are found in more or less irregular palmelloid colonies embedded in mucilage which is structureless (*Aphanocapsa* (fig. 187, A), *Microcystis* (fig. 186)) or exhibits differentiation of special, often stratified, sheaths to the individual cells (*Gloeocapsa* (fig. 187, B–E)). In other cases the cells of these colonial forms assume a definite arrangement, forming 1-layered plates as in *Merismopedia* (fig. 184, B, C) or being distributed at the periphery of gelatinous spheres, as in *Coelosphaerium* (fig. 185, A). These unicellular and colonial types are grouped as the Chroococcales, but a large number of Myxophyceae (the so-called Hormogoneales) assume the habit of simple or branched filaments.

The simple filamentous types are comprised in the Oscillatoriaceae, of which the common *Oscillatoria* (fig. 191) affords a good example; here the trichomes are naked, but in *Lyngbya* (fig. 193, A–C) they are encased in a firm and often thick mucous

[1] Etard and Bouilhac, Comptes Rendus, CXXVII, 1898, p. 119; Schindler, Zeitschr. f. Bot. V, 1913, p. 553.

[2] cf. Fritsch, Geogr. Journ. 1907, p. 533 et seq.; and Journ. of Ecol. X, 1922, p. 232.

[3] The *Pedras negras* of Angola are due to the prolific growth of *Scytonema Myochrous* var. *chorographicum* (W. & G. S. West, Journ. of Bot. 1897, p. 303); cf. also Diels, Ber. Deutsch. Bot. Ges. XXXII, 1914, p. 502; Bews, Ann. Natal Museum, III, 1917, p. 553, and Journ. of Ecol. IV, 1916, p. 132.

sheath[1]. In the allied genus *Phormidium* (fig. 193, D) the filaments are agglutinated by their more or less diffluent sheaths to form large flat irregular expanses (often covering an area of a square foot and more) adhering to rock-surfaces, soil, etc. In *Microcoleus* (fig. 194, A) and *Schizothrix* (fig. 195, A, B) several or many trichomes are contained within a common sheath which is often branched.

In all these cases there is little or no differentiation among the cells of the trichomes, and nearly all of them are capable of growth and division. In most of the filamentous Myxophyceae, however, the trichomes are interrupted at more or less frequent intervals by slightly larger cells which have firmer, often thickened, walls and usually yellowish or colourless contents, and which have lost the power of growth and division; these are the *heterocysts* (fig. 197, *h*) which are considered more fully below. In the common *Nostoc* (fig. 196), for example, where numerous contorted moniliform trichomes are embedded in extensive gelatinous masses of varying shape, spherical heterocysts are intercalated at intervals between the ordinary vegetative cells, whilst in *Cylindrospermum* (fig. 197, E–G) a single heterocyst is found at one end of each trichome. Heterocysts are also present in the majority of the branched filamentous types.

Many of these (Scytonemataceae) show false branching; the trichomes of the main filament rupture at intervals and, after perforating the sheath, grow out as branches which secrete a sheath of their own. *Tolypothrix* (fig. 199, E) commonly forms these pseudo-branches singly and one or more heterocysts are found in the main trichome just above the point of branching. In *Scytonema* (fig. 199, A), where the branches are often paired, there is no such relation to the heterocysts. True branching by lateral outgrowth of cells of the main trichome is seen in the Stigonemataceae, e.g. *Hapalosiphon* (fig. 205) and the more complex *Stigonema*, where usually several rows of cells occur within the sheaths (fig. 206, B) and the heterocysts in part occupy a peculiar lateral position (fig. 206, C).

A whole family of the Hormogoneales (the Rivulariaceae) are characterised by the attenuation of the trichomes to a hair-like point, and in these one or more heterocysts are generally located at the base of each trichome (cf. figs. 201, 202); the filaments in this family usually exhibit false branching.

After this preliminary survey a more detailed consideration of certain features may be undertaken. The *cell-structure* has aroused unlimited controversy and to discuss all the views that

[1] It is customary in these cases to speak of the entire structure as a *filament*, whilst the contained thread is designated the *trichome*.

have been put forward would be out of place here[1]. A great part of the protoplast would usually appear to exhibit an alveolar structure (fig. 182, A), the alveoli according to Baumgaertel[2] being occupied by a substance of mucilaginous or more or less stiff gel-like consistency. In the vast majority of cases two regions are readily distinguished within the protoplast, a peripheral one in which the pigment is located and a colourless central body (West's "incipient nucleus"); in some cases these are recognisable in the living cell. The central body can generally be brought out by treatment with Eau de Javelle and subsequent staining with methylene blue[3]. In the filamentous types its surface is often irregular, numerous processes being extended into the peripheral pigmented region; but this does not appear to be the case in the Chroococcaceae[4].

The application of the term "nucleus" to this central body has been a matter of much debate. All authorities are agreed that there is neither nuclear membrane nor nucleolus and that, if it is to be regarded as a nucleus, it is one of a simple type. It contains granules which, according to most investigators, are of the nature of chromatin[5], an opinion however which Fischer[6] does not share; in many of the simpler colonial forms the granules of the central body do not give pronounced chromatin-reactions and such have been termed metachromatin granules[7]. Miss Acton[8], in her investigations on the cytology of the Chroococcaceae, believed she had found a transition from a state in which the central region is scarcely differentiated and includes only occasional granules giving a chromatin reaction (*Chroococcus turgidus* (fig. 182, A)), to a definite "nucleus" containing an accumulation of chromatin or of some substance allied to it; such a "nucleus" is either only evident at the time of division (*Merismopedia elegans* (fig. 1, G)) or always present (*Chroococcus macrococcus*). These results correspond to a considerable extent to those of Gardner. No doubt similar differences are observ-

[1] Summaries will be found in several of the papers mentioned below (cf. especially Olive).

[2] Archiv f. Protistenkunde, XLI, 1920, p. 101.

[3] cf. Lemmermann, 1910, p. 8; see also McLean, New Phytol. XIII, 1914, p. 71; Geitler, 1925, p. 46.

[4] cf. Acton, Ann. of Bot. XXVIII, 1914, p. 433.

[5] cf. for example Scott, Journ. Linn. Soc., Bot. XXIV, 1887, p. 188; Kohl, Üb. d. Organisation u. Physiol. d. Cyanophyceenzelle, etc. Jena, 1903; Olive, Beihefte Bot. Centralbl. XVIII, 1904, p. 35; Gardner, Univ. California Publ., Bot. II, 1906, No. 12, p. 261.

[6] Bot. Zeit. LXIII, 1905, p. 74; cf. also Palla, Jahrb. wiss. Bot. XXV, 1893, pp. 523 and 556; recent workers (Baumgaertel, Haupt) express no definite opinion on this point.

[7] cf. Acton, loc. cit. p. 448. [8] loc. cit. p. 450; cf. also Gardner, p. 262.

able in the more advanced forms and may account for some of the discrepancies between the conclusions of earlier investigators whose work has been largely confined to the filamentous types; moreover some of the results may apply to more or less abnormal material kept in the laboratory under unfavourable conditions.

Many workers (Zacharias[1], Gardner, loc. cit., Guillermond[2], Acton, loc. cit.) appear to be agreed that there is no mitotic division of the central body, whilst Hegler[3], Kohl (loc. cit. p. 173), Phillips[4], and Olive (loc. cit. p. 30) believe to have recognised a rudimentary spindle and chromosomes. Wager[5] describes a modified mitosis with bodies of the nature of chromosomes. Zacharias is of the opinion that the chromosomes of these investigators are ridges or projections of the central body.

According to Fischer (loc. cit. p. 106) the glycogen produced in photosynthesis accumulates in the central region and here gives rise to another carbohydrate (anabaenin), which appears in masses simulating chromosomes. This interpretation has not been supported by other investigators.

It is scarcely possible to arrive at any satisfactory conclusion from amid this conflict of views, but it may probably be gleaned that anything approaching the true mitosis of higher plants is lacking, though in some of the filamentous Myxophyceae chromatin-aggregations resembling chromosomes may possibly occur. It would seem that within the class various phases in the differentiation of a nucleus are to be found[6], and the real difference of opinion centres around the question as to how far its evolution has progressed. It is perhaps well to emphasise that, amongst those who have dealt with this problem in the present century, Fischer and Geitler[7] are practically the only ones to deny completely the nuclear nature of the central body, whilst all the most recent investigations[8] have failed to give any support to the occurrence of anything approaching mitosis.

With reference to the peripheral pigmented region there is more agreement, and much of the discussion as to whether it is to be called a chromatophore or not appears to the outsider as a quibble over a name. There seems to be no doubt that there is

[1] Jahrb. Hamburg. Wiss. Anstalten, XXI, 1903, p. 54 et seq.; cf. also Bot. Zeit. LXV, 1907, Abt. 2, p. 284.

[2] Rev. gén. de Bot. XVIII, 1906, p. 453.

[3] Jahrb. Wiss. Bot. XXXVI, 1901, p. 325.

[4] Contrib. Bot. Lab. Univ. Pennsylvania, II, No. 3, 1904, p. 296.

[5] Proc. Roy. Soc. London, LXXII, 1903, p. 406.

[6] cf. also Sharp, Cytology, New York, 1921, p. 206.

[7] Archiv f. Protistenkunde, XLV, 1922, p. 416.

[8] cf. Baumgaertel, loc. cit. p. 138; Haupt, Bot. Gaz. LXXV, 1923, p. 183; Schwellengrebel, Quart. Journ. Micr. Sci. LIV, 1910, p. 626.

no definitely differentiated chromatophore[1] such as holds the pigments in most other plants, but in this connection it is well to remember that in several Isokontae (*Sphaerella*, p. 60, *Hydrodictyon*, p. 116) the chromatophore is likewise very ill-defined. It would seem that the pigments are lodged in innumerable minute granules[2], and various workers (Hegler, Kohl) have regarded these as the actual chromatophores (cyanoplasts), but they are more likely to be identical with the grana of the chromatophores of other plants. It seems doubtful whether any part of the peripheral cytoplasm is devoid of pigment, but Fischer believed he had seen such a non-pigmented cytoplasmic lining.

The pigments themselves comprise chlorophyll, the yellow carotin, the blue-green *phycocyanin*, and a red pigment closely allied to the phycoerythrin of the Rhodophyceae[3]. The phycocyanin is responsible for the prevalent blue-green coloration of members of this class; it is soluble in water and by appropriate means can be extracted from the dead cells[4]. The varied tints shown by different Myxophyceae, as well as by the same species at different times, are due to the diverse proportions in which the four above-mentioned pigments occur; thus, when both phycocyanin and phycoerythrin are present, violet shades are obtained, whilst when the latter predominates the colour is more reddish. Attention may however be drawn to the fact that colorations other than blue-green are as often due to special pigments in the sheaths as to variation in the pigmentation of the protoplast.

Gaidukov[5] was the first to show that some species of *Oscillatoria* take on a colour complementary to that of the light to which they are exposed. He interpreted the frequent red coloration of deep-water Cyanophyceae[6] as an adaptation to the quality

[1] In *Glaucocystis* and *Gloeochaete* there are properly differentiated chromatophores, but it is exceedingly doubtful whether these forms are related in any way to the main mass of the Myxophyceae; cf. p. 493.

[2] Some writers however speak of their being diffused through the peripheral cytoplasm, whilst others describe the phycocyanin as diffused and the remaining pigments as occurring in granules.

[3] cf. Boresch, Ber. Deutsch. Bot. Ges. XXXIX, 1921, p. 93, where earlier references are given, and Boresch, Biochem. Zeitschr. CXIX, 1921, p. 167. The phycoerythrin of Myxophyceae differs from that of Rhodophyceae in its absorption-spectrum. Wille (Ber. Deutsch. Bot. Ges. XL, 1922, p. 188) has, however, recorded true phycoerythrin in *Phormidium persicinum* Gom.

[4] Kohl (loc. cit. p. 77) recommends treatment with chloroform-water.

[5] cf. Ber. Deutsch. Bot. Ges. XXI, 1903, p. 484, and XLI, 1923, p. 356; also Dangeard, Comptes Rendus, CLIII, 1911, p. 293, and Boresch, Archiv f. Protistenkunde, XLIV, 1922, p. 1.

[6] For some striking instances, see Geitler, Int. Rev. d. ges. Hydrobiol. u. Hydrogr. X, 1922, p. 687; and Pascher, Bot. Archiv, III, 1923, p. 311.

of the light reaching these depths. Red coloration is however characteristic of several planktonic Myxophyceae (e.g. of the marine *Trichodesmium erythraeum* Ehrenb., whose occasional abundance has given the name to the Red Sea), as well as of some forms which inhabit terrestrial situations. Whilst the diverse shades exhibited by the members of this class may in part be the result of chromatic adaptation, there is evidence to show that changes of pigmentation may also result from varying light-intensities, as well as from a paucity of nutritive salts and especially from nitrogen-starvation[1].

The first evident products of photosynthesis are sugars and glycogen[2]. Fischer's views with reference to the transformation of the latter into an insoluble carbohydrate, anabaenin, within the central body have already been mentioned (p. 438). Starch never occurs, but minute drops of oil are frequent. The cells of the Myxophyceae often contain an abundance of granules[3], and these are no doubt of several kinds, but it is not easy to reconcile the opinions of different writers as to their nature. It appears possible to distinguish clearly between central granules (α granules of Gardner, loc. cit.) and *cyanophycin* granules (β granules of Gardner). The former occur in the central body, the latter only in the peripheral region, often especially near the cell-wall. Both are apparently albuminous in nature, containing both nitrogen and phosphorus, the central granules possibly consisting largely of some nucleo-protein and being analogous to the metachromatin-granules dealt with above. The cyanophycin granules appear, on the other hand, to be a form of protein-reserve (crystalloids), since they disappear in the dark, are consumed during cell-division, and occur in large quantities in the spores. They are easily dissolved by weak acids which leave the central granules unaffected. They constitute glistening, usually rounded or subangular, bodies which readily stain with picro-carmine or brilliant blue or a dilute aqueous solution of neutral red, whilst the central granules are easily brought out with methylene blue, which does not affect the others[4].

[1] cf. especially Schindler, Zeitschr. f. Bot. v, 1913, p. 497; Magnus and Schindler, Ber. Deutsch. Bot. Ges. xxx, 1912, p. 314.

[2] According to Baumgaertel (loc. cit. p. 98) the glycogen is immediately converted into glycoproteins; cf. also Geitler, 1925, p. 3.

[3] In diagnoses of Myxophyceae it is usual to describe the protoplast as granular or non-granular. It is however very doubtful whether this is a taxonomic character of any value, since the state of the protoplast in this respect almost certainly depends on the previous conditions of nutrition.

[4] Baumgaertel (loc. cit.), in his researches on the cell-structure of the Blue-green Algae, recognised three kinds of inclusions in the protoplast. In the central body (centroplasm) the alveoli are occupied by endoplasts which may be of very diverse shape and are of gel-like consistency, whilst

The protoplast of the Myxophyceae is ordinarily devoid of evident vacuoles, and it is probable that, in most species at least, such only occur when the cells are in a moribund condition; they appear for example in the developing hair-cells at the ends of the trichomes of the Rivulariaceae. In view of recent work on *Pleurococcus*, this absence of large vacuoles may well be connected with the obviously widespread faculty of members of this class to survive prolonged periods of desiccation with little alteration.

Much discussion has centred around the so-called *pseudovacuoles* which occur—usually in considerable numbers—in the cells of many planktonic Myxophyceae (*Microcystis*, *Coelosphaerium*, *Anabaena*, *Aphanizomenon*, etc.) and appear under low powers as black dots, whilst under higher powers they have a dark-red appearance. They have been interpreted as gas-vacuoles, a view which receives considerable support from recent experiments of Klebahn's[1], although the fact that they do not disappear when the Algae in question are placed in a vacuum[2], is not altogether easy to explain on this basis. They have also been regarded as of an oily nature. Whatever they may be, there seems little doubt that they materially contribute to the buoyancy of the forms possessing them[3], although they are not restricted to planktonic types[4]. They also occur in the hormogones (p. 446) of *Nostoc*, *Phormidium*, and *Lyngbya*, especially when exposed to strong light[5], and this fact, taken together with their apparent diminution in the plankton-forms when cultivated in the dark, has led Lemmermann to suggest that they may serve as a light-screen.

The cells are invariably provided with a definite membrane which is however not always readily recognisable in young stages, especially in those forms which are embedded in mucilage. In

apposed to them and lying within the cytoplasmic lamellae are the spherical epiplasts readily stained with methylene blue and equivalent to the central granules of other workers. In the peripheral region (chromatoplasm) are the ectoplasts (= cyanophycin granules). According to Baumgaertel the highly refractive granules found in the spores are not cyanophycin-granules, but endoplasts; cf. also Geitler, 1922, loc. cit.

[1] Jahrb. Wiss. Bot. LXI, 1922, p. 535, and Ber. Deutsch. Bot. Ges. XLIII, 1925, p. 143.

[2] cf. Molisch, Bot. Zeit. LXI, 1903, p. 51.

[3] The facts mentioned by Lemmermann (1910, p. 11) do not appear to disprove this view; moreover the writer has material of *Microcystis*, *Aphanizomenon*, and other forms, that has been in 4% formalin for nigh upon 20 years and still floats at the surface. See also van Goor, Revue Algol. II, 1925, p. 19.

[4] cf. Brand, Ber. Deutsch. Bot. Ges. XIX, 1901, p. 158.

[5] Lemmermann, 1910, p. 12.

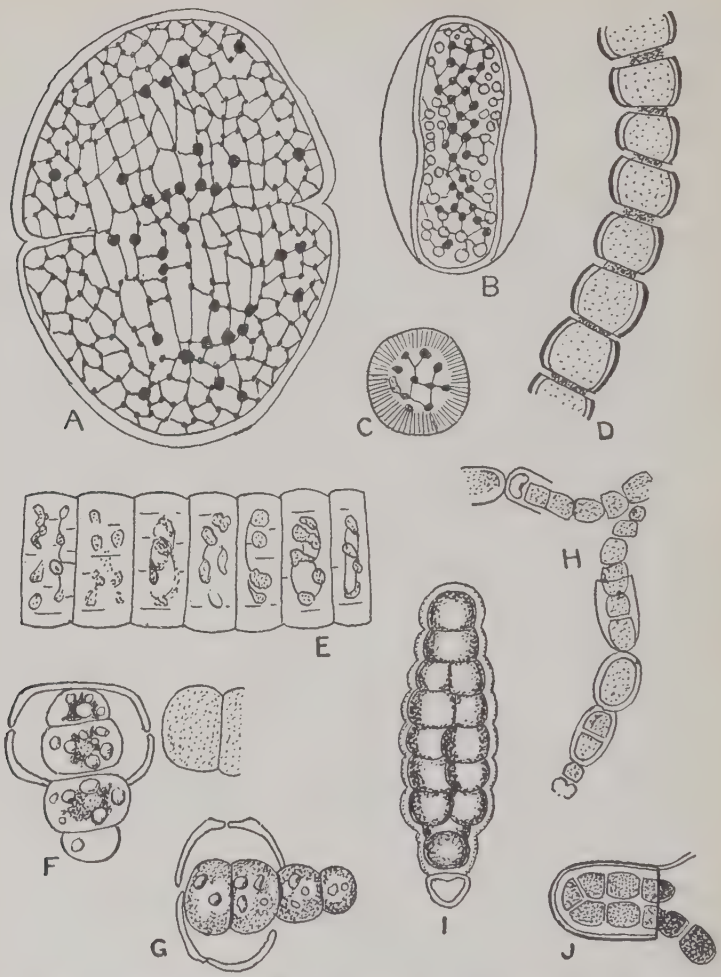

Fig. 182. A, *Chroococcus turgidus* (Kütz.) Naeg., dividing cell, stained to show the internal structure (after Acton, ×2500). B, *Aphanothece prasina* A.Br., the same (after Acton, ×2500). C and E, *Oscillatoria* sp. (after Olive); C, cross-section; E, longitudinal section. D, *Anabaena* sp., showing cell-sheath and inner investment (after Fritsch, ×2300). F and G, *Nostoc commune* Vauch., germinating heterocysts (after Geitler, ×2500). H, *Anabaena Azollae* Strasb., filament with germinating spores (after Fritsch, ×680). I, *Nostoc commune* Vauch., germinating hormogone (after Geitler, ×900). J, *Cylindrospermum licheniforme* (Bory) Kütz., germinating spore (after Bristol, ×825).

older cells, particularly in many of the filamentous forms, the investment is clearly distinguishable into two parts, the *inner investment* (Lemmermann's "Hautschicht"), which envelopes the protoplast on all sides, and the *cell-sheath* (Lemmermann's "Wandschicht"). The latter may completely surround the cells, as in the Chroococcaceae, or form a cylindrical sheath which is either continuous (*Oscillatoria*) or interrupted between the cells (*Anabaena* (fig. 182, D))[1]. Whilst the inner investment appears merely as a somewhat modified plasmatic membrane, the cell-sheath is a firmer portion of the mucilage-envelope or may, as in *Oscillatoria*, represent it alone. In other words it is homologous with the secondary mucilage-envelopes, not in direct contact with the protoplast, which are developed in so many Myxophyceae and form the strata in the sheath of a *Gloeocapsa* or the firm sheaths of *Lyngbya*, *Scytonema*, etc. The septa appear to consist of the inner investment only, although whether this is always the case is not clear. Most of the statements in the literature refer to the cell-sheath which, like the mucilage, in young cells probably consists mainly of pectic compounds; cellulose is however frequently present in the sheath (e.g. in species of *Schizothrix* and *Phormidium*), which then gives a blue coloration with chlor-zinc-iodide[2]. The firm cell-sheath of older individuals and the specialised sheaths of many Oscillatoriaceae include compounds which render them very resistant[3]. The thick sheaths found in many of the Hormogoneales and in some of the Chroococcales are often coloured yellow or brown; other shades (red, violet) also occur, but are rarer.

Brand[4] has drawn attention to the fact that the ordinary Cyanophyceous cell does not readily plasmolyse. When placed in hypertonic solutions, the entire cell often undergoes slight irregular contraction, the membrane not separating from the protoplast at all or only doing so at a few points. These features are no doubt to be related to the absence of vacuoles, as well as to the elasticity of the membranes in the young cells.

Many workers have described protoplasmic continuity[5]

[1] Fritsch, Beih. Bot. Centralbl. XVIII, 1905, p. 194; Lemmermann, 1910, p. 3. Geitler (Beih. Bot. Centralbl. XLI, 1925, p. 192; see also Geitler, 1925, p. 11) distinguishes two types of membranes in the Myxophyceae, but the writer is not of the opinion that the distinction can be maintained.

[2] cf. Lemaire, Journ. de Bot. XV, 1901, p. 255; and Virieux, Comptes Rendus, CLI, 1910, p. 334.

[3] The most recent investigation of the chemical nature of the envelopes of Myxophyceae is that of Klein (Sitz.-ber. Akad. Wiss. Wien, Mat.-nat. Kl. CXXIV, 1915, p. 529); he denies the presence of chitin which several earlier workers (Hegler, Kohl) had affirmed.

[4] Ber. Deutsch. Bot. Ges. XXI, 1903, p. 302.

[5] cf. e.g. Borzi, Malpighia, I, 1887, p. 74.

between the cells of the Hormogoneales, and such is clearly apparent in many Stigonemataceae (cf. fig. 206, D), where each cell is completely enveloped by a cell-sheath; the pores are particularly conspicuous in *Stigonema ocellatum* if the plants are first dried and subsequently soaked in water. In other Hormogoneales, however, the question of protoplasmic continuity requires further investigation, as the statements in the literature are very conflicting; amongst recent workers Phillips[1] affirms its occurrence, whilst Gardner[2] failed to find any protoplasmic connections in the forms he investigated. Fritsch[3] has suggested that the intercellular portions of the inner investment have been interpreted as protoplasmic connections in some of these forms.

In healthy material, especially of the filamentous genera, a very large percentage of cells are usually found in process of division. The Chroococcaceae are stated to divide by a progressive constriction of the cell, whilst in the filamentous types a septum gradually grows inwards from the periphery dividing both the pigmented cytoplasm and the central body into two. In some cases, however, it appears that the latter begins to constrict, or even divides, before any division of the cytoplasm is apparent (e.g. in *Chroococcus macrococcus*[4] and some of the filamentous forms), and such cases no doubt indicate a certain individuality on the part of the central body.

The *heterocysts*[5], which (with few exceptions) occur in all the Hormogoneales except the Oscillatoriaceae, exhibit practically the same structure in all cases. They are generally enlarged cells with a well-defined somewhat thickened wall, which is composed of cellulose; according to Geitler there is an external layer of pectic substance constituting the original cell-membrane, the cellulose forming a thickening-layer on its inner side. The heterocysts are commonly solitary, but in species of *Tolypothrix* (fig. 199, E), *Calothrix*, *Nostoc*, etc. they are often formed in series. When the heterocysts occupy an intercalary position, the wall is frequently slightly thicker at the two poles (figs. 197, 199), where a prominent pore connecting with the adjacent vegetative cells is recognisable; when the heterocyst is terminal, only one such polar thickening and pore occur, viz. on the side adjacent to the filament. The heterocysts develop

[1] loc. cit. p. 299.

[2] loc. cit. p. 274; cf. also Baumgaertel, loc. cit. p. 140.

[3] loc. cit. p. 196.

[4] Acton, loc. cit. p. 447; cf. also Olive, tab. II, fig. 73.

[5] Brand, Ber. Deutsch. Bot. Ges. XIX, 1901, p. 153, and Beih. Bot. Centralbl. XV, 1903, p. 38; Fritsch, New Phytol. III, 1904, p. 86; Geitler, Sitz.-ber. Akad. Wiss. Wien, Mat.-nat. Kl. CXXX, 1921, p. 223.

from the ordinary vegetative cells, and, during the differentiation of the wall, the peripheral region of the cytoplasm loses its pigment[1] and takes on a yellowish colour. For a considerable period the protoplast remains united with that of the adjoining vegetative cell or cells by broad protoplasmic connections passing through the pores. According to Geitler the cytoplasm undergoes little change for some time after the complete differentiation of the heterocyst, except for the disappearance of the pigment already mentioned; ultimately degeneration sets in and the protoplasmic contents gradually vanish.

In many cases, during the development of the heterocyst, a bright highly refractive granule appears internal to each pore; these granules persist even after the death of the protoplast. They are usually situated on the inner side of a delicate membrane which completely surrounds the protoplast, more rarely between it and the cellulose-wall. Various opinions have been held as to the function and nature of these granules. While Hegler (loc. cit. p. 305) regarded them as reserve-substances, Kohl compared them physiologically with the masses of callus occluding the sieve-plates of higher plants. Many investigators have identified them with cyanophycin-granules, but according to Baumgaertel (loc. cit. p. 140) and Geitler they are partly of the nature of "epiplasts" and partly "ectoplasts."[2] Geitler also draws attention to the fact that similar granules often occur in corresponding positions in the vegetative cells (cf. especially *Lyngbya bipunctata* Lemm. and fig. 191, F), and he is disinclined to ascribe any special function to them.

In view of their characteristic structure and the definite position they often occupy in the threads (cf. p. 436), there has been much speculation as to the nature and purpose of heterocysts. They have been regarded as a means of limiting the length of the filaments (Borzi, Kohl), and there is no doubt that in some Myxophyceae their formation conditions the breaking up of the trichome into hormogones; in many heterocystous forms, however, this occurs without their cooperation. Another view regarded them as storehouses for reserve-substances (Hegler, Fritsch). Recent observations (Brand, Spratt, Geitler) have lent a good deal of support to the view that they represent archaic reproductive cells, now largely functionless, but under certain circumstances still fulfilling their old rôle. Brand[3] was the first to describe, in species of *Nostoc*, the setting free of the

[1] In species of *Rivularia*, however, the heterocysts retain their pigment for long periods, and the writer has observed the same phenomenon in tropical material of other genera.

[2] See p. 440, footnote 4.

[3] Brand, loc. cit. 1901, p. 154.

contents of the heterocysts as gonidia which subsequently developed into new filaments. Similar observations were made by Spratt[1] in the case of *Anabaena Cycadearum*, whilst recently Geitler[2] has recorded germination of the contents of the heterocysts in a number of species belonging to the genera *Nostoc* (fig. 182, F, G), *Anabaena*, and *Tolypothrix*. Geitler describes the reappearance of pigment in the protoplast and regards the cellulose-layer of the heterocyst as a reserve, having observed its disappearance when germination of the contents was taking place.

It must be understood, however, that such instances of germination of heterocysts are extremely rare and no case is known in which they occur even commonly. They give more the impression of abnormal occurrences than of a return to an old practice. There is moreover no parallel elsewhere for the wholesale persistence and regular development of an aborted reproductive organ. One cannot help feeling that the real function of the heterocyst is still undiscovered. The frequent, though by no means invariable, juxtaposition of heterocysts and spores (*Cylindrospermum* (fig. 197, E–G), *Gloeotrichia* (fig. 203, A), many species of *Anabaena* (fig. 197, B, D)) is perhaps a significant feature.

The multiplication of the unicellular and colonial Blue-green Algae is brought about principally by simple cell-division, which may take place in every direction of space (*Aphanocapsa*, *Gloeocapsa*) or in certain directions only (*Merismopedia*, *Gloeothece*). The definite or indefinite colonies thus produced dissociate into smaller groups on attaining a certain size. In all the filamentous forms multiplication is largely effected by the formation of so-called *hormogones*. These are short lengths of trichome, exhibiting no special differentiation, which are generally set free from the extremities of the filaments or their branches and by division develop into new plants. In some cases, as already mentioned, they are limited by the heterocysts (*Nostoc*). Many of the filamentous forms break up at times into a series of hormogones, owing to the secretion at intervals of an intercellular substance which is at first dark green, but may later become colourless and highly refractive (fig. 191, E)[3]. These *separation-discs* are in general biconcave in shape, but may be so thin in the middle as to appear as a mere ring. In other cases hormogones are formed by the dying away of certain cells,

[1] Ann. of Bot. xxv, 1911, p. 376.

[2] loc. cit. p. 234.

[3] cf. Brand, Beih. Bot. Centralbl. xv, 1903, p. 49; and Ber. Deutsch. Bot. Ges. xxiii, 1905, p. 62.

which first become compressed by the adjacent living cells and then disintegrate (Brand's *necridia*). The extensive strata produced by many Hormogoneales are a result of rapid growth of the filaments, combined with repeated hormogone-formation[1].

The hormogonia invariably exhibit slow motion, which takes place in a straight (*Lyngbya*, *Nostoc*, *Rivularia*, *Scytonema*, etc.) or spiral line (*Oscillatoria*, *Arthrospira*)[2]. Similar slow spontaneous movements on the part of the ordinary trichomes are met with in a few of the Oscillatoriaceae. They are most conspicuous in *Oscillatoria*[3], and their rapidity is enhanced by increase of temperature or of the intensity of the light. The motion consists of a slow creeping or gliding of the trichome forwards or backwards in the direction of its longitudinal axis, accompanied by rotation and often by a slow oscillation of the upper part; each oscillation commonly terminates with a more rapid bending of the extreme apex. In some cases only the oscillation is observed, without the forward progression. In *Arthrospira* (fig. 191. G) the movements are more vigorous, though spasmodic and jerky. In *Spirulina* there is a well-marked rotation around the axis of the spirally twisted trichomes, as they progress through the water.

Although these movements have been much studied, especially those of the Oscillatoriaceae, no convincing explanation as to the mechanism has yet been offered. It would seem that in most, if not all, cases contact with a solid body or with the surface film of water is necessary. The filaments of many of the species concerned secrete a small quantity of soft mucilage, and this has been regarded as playing some rôle in the movement (cf. Fechner, loc. cit.). Whilst this view perhaps finds most support, Schmid (loc. cit. 1923, p. 411) believes in the occurrence of rhythmic longitudinal waves, conditioned by changes in the density of the protoplasts, and traversing the filaments from end to end. Phillips (loc. cit. p. 318) records short cilia along the sides of the trichomes of *Oscillatoria*, an observation which is uncorroborated.

Resting spores (akinetes) have been observed in many of the filamentous forms, but among the Chroococcales are not known except in *Gloeocapsa*. It is only in certain Nostocaceae and

[1] In some Scytonemataceae and Stigonemataceae short hormogonia, which are completely enclosed in a thick-walled and stratified sheath, are formed (Borzi's *hormocysts*).

[2] cf. Brand, loc. cit. 1903, p. 53 et seq., where the earlier literature is considered.

[3] cf. Correns, Ber. Deutsch. Bot. Ges. xv, 1897, p. 139; Fechner, Zeitschr. f. Bot. vii, 1915, p. 328; Schmid, Flora, cxi, 1918, p. 327, and Jahrb. Wiss. Bot. lx, 1921, p. 572, and lxii, 1923, p. 328.

Rivulariaceae, however, that they appear with sufficient regularity to make them of value for taxonomic purposes. In the development[1] of these spores a vegetative cell usually increases more or less appreciably in size, becoming stocked with food-reserves and developing a distinct exospore and endospore which correspond respectively to cell-sheath and inner investment of the ordinary cell; the exospore is thick and often yellow or brown in colour. Such spores can remain dormant for very long intervals of time[2]. They are commonly spherical or cylindrical and are either produced singly (fig. 197, C) or in chains (fig. 197, D); in the heterocystous forms, they are often developed in contact with the heterocysts (figs. 197, E–G; 203, A). In germination[3] division of the protoplast may (fig. 182, H) or may not occur before it is liberated from the spore-membranes. In some few cases the latter become mucilaginous and the protoplast divides within the mucus thus formed, but as a general rule a small part of the membrane becomes diffluent or gets detached as a lid (fig. 182, J) and the new filament gradually protrudes from the remaining part of the spore-wall. In certain species of *Nostoc* Bristol observed a division of the protoplast in all directions, with the formation of a more or less spherical cell-cluster; this is however probably to be interpreted as a closely coiled trichome confined within the mucilage formed by the spore-membranes.

In a number of genera of Myxophyceae so-called *gonidia*[4], which are probably comparable to the aplanospores found in other classes, are encountered. They are only met with at all regularly in the series of the Chamaesiphonales (cf. p. 465), a somewhat specialised group of unicellular and filamentous forms distinguished by their attached habit and polarity (differentiation of base and apex). The gonidia are here produced within sporangia originating from the ordinary vegetative cells, which often exhibit some preliminary increase in size. Rejuvenescence of the protoplast takes place, and this is generally followed by division whereby a considerable number of gonidia are formed. The division may take place in all directions (*Gomphosphaeria*, *Pleurocapsa*, *Oncobyrsa*) or only in the transverse plane (*Chamaesiphon* (fig. 190, on the right)). In *Chamaesiphon* the development of the gonidia is peculiar in so far as

[1] cf. Brand, loc. cit. 1903, p. 32; Fritsch, loc. cit. 1905, p. 200.

[2] Bristol, New Phytol. XVIII, 1919, p. 92.

[3] Fritsch, New Phytol. III, 1904, p. 218 et seq.; Bristol, 1920, p. 51.

[4] Geitler (1925, p. 21) speaks of these structures as endospores and exospores according to their mode of formation, but it would appear best to restrict the term spore in Myxophyceae to the resting cells above described.

the protoplast of the sporangium continues to grow and successive gonidia are abstricted from its upper end (cf. also p. 468). Among the Hormogoneales gonidia, formed singly within the parent-cell, are recorded for *Anabaena Azollae* Strasb. (Fritsch, loc. cit. 1904, p. 224), *Phormidium uncinatum* Gom. (Brand, loc. cit. 1903, p. 46), and *Lyngbya aerugineo-coerulea* Gom.[1] The gonidia are usually spherical and develop a thin membrane, either before or after liberation from the sporangium.

In *Nostoc punctiforme* Sauvageau[2] described reproduction by small cells with a thin membrane (cocci), apparently ordinary vegetative cells. They formed a scum on the surface of the water and each one was found capable of producing a colony.

In no class of the Algae have there been so many records of *polymorphism* as in the Cyanophyceae. This is due to the fact that large numbers of diverse forms often occur together forming a composite stratum, so that on superficial investigation the passage of one form into another is readily imagined. G. S. West[3] long ago pointed out that the erroneous statements of Hansgirg, Wolle, and others, according to which the Chroococcales were stages in the development of the more highly organised forms, were due to many of the colonial Myxophyceae frequenting similar habitats to those occupied by the higher filamentous types. In many cases in fact the former are the precursors of the latter in the colonisation of terrestrial substrata. A consideration of the older views on polymorphism would nowadays be out of place, and it is sufficient to say that they are neither supported by pure cultures, nor by accurate observation of the diverse forms where they occur together. There is rarely much difficulty in discriminating between the stages in the development of the filamentous types and the unicellular or colonial Chroococcales.

Some general remarks on the distribution and mode of occurrence of the Myxophyceae have already been made above (p. 434). These may now be supplemented by further details, although lack of space forbids more than a cursory treatment. Blue-green Algae are found everywhere in damp and wet habitats and many of them are almost entirely subaerial in habit, occurring in every conceivable situation on rocks, stones, and the trunks of trees. The Chroococcales and species of *Nostoc* appear as more or less gelatinous masses of diverse hues, whilst the filamentous species frequently form compact felt-like, mucous, leathery, or even cartilaginous patches of various

[1] Fritsch, in Rep. Nat. Antarct. Exped. VI, 1912, p. 28.
[2] Ann. sci. nat. Bot. 8 sér. III, 1897, p. 367.
[3] Journ. of Bot. 1899, p. 52.

colours and of considerable extent—often on the vertical faces of rocks which are kept permanently moist (cf. footnote on p. 435). Diverse Chroococcales, together with species of *Nostoc*, *Scytonema*, and *Stigonema*, occur amongst Mosses and Liverworts in the deep gullies and glens of mountainous regions.

Various Myxophyceae, principally of the genera *Nostoc*, *Scytonema*, and *Gloeocapsa*, are the algal constituents of Lichens, the forms in question being usually much modified and often losing almost all traces of their original specific characters. *Anabaena Azollae* Strasb. lives within mucilage-cavities of the leaves of *Azolla*, *A. Cycadearum* Reinke within the root-tubercles of *Cycas*[1], while species of *Nostoc* inhabit similar hollows in the thalli of *Blasia* and *Anthoceros*. A symbiosis between nitrogen-fixing Bacteria and the Blue-green Algae of the subterranean soil-community is very probable[2].

As already mentioned, Myxophyceae constitute the principal vegetation of hot springs[3]. Certain of the Algae involved play a considerable part in the formation of rock-masses by the precipitation of carbonate of lime or of silica from the water. The deposits formed around the hot springs in many parts of the world consist of brightly coloured basins or terraces of travertine or sinter. All shades of yellow, orange-red, pink, blue, and blue-green occur and are due to the presence of the brilliantly coloured Algae within the deposit. In the case of the travertine the deposition of the carbonate of lime is due very largely to the extraction by the Algae of the carbon dioxide dissolved in the water, as was first shown by Cohn (loc. cit.). Weed[4] has described the rôle of Myxophyceae in the production of the travertine and sinter deposits of the Yellowstone National Park; according to him 1·25 to 1·5 mm. of travertine are formed in three days. The character and colour of the deposit depend upon the temperature of the water and the situation of the spring or geyser. *Phormidium laminosum* has been stated to occur at as high a temperature as 87·5° C.

On the shores of the Great Salt Lake, Utah, species of *Gloeocapsa* and *Gloeothece* are responsible for the formation of oolitic calcareous grains[5], whilst *Schizothrix fasciculata* forms spherical calcareous pebbles on the bottom of Lough Belvedere, near

[1] cf. Spratt, Ann. of Bot. xxv, 1911, p. 369; Life, Bot. Gaz. xxxi, 1901, p. 265.

[2] cf. Bristol, 1920, p. 56, where the earlier literature is considered.

[3] Cohn, Abhandl. Schles. Ges. f. vaterl. Kultur, 1862, p. 35; Tilden, Bot. Gaz. xxiv, 1897, p. 194; G. S. West, Journ. of Bot. xl, 1902, p. 241.

[4] Rep. United States Geol. Survey, ix, 1887–8, p. 619.

[5] Rothpletz, Bot. Centralbl. li, 1892, p. 265.

Mullingar in Ireland[1]. The oolitic particles found in various geological strata may have had a similar origin[2]. Certain species of *Schizothrix* (e.g. *S. coriacea*) have their strata customarily encrusted with carbonate of lime, whilst in *Rivularia dura* particles of lime are deposited within the mucilage of the colonies.

Cyanophyceae also play a big rôle in ordinary freshwaters. Many of the Oscillatoriaceae emit a very disagreeable odour, and ponds and ditches which contain quantities of *Oscillatoria* often have an objectionable smell. Species of *Phormidium* and various Chamaesiphonales are important constituents of the attached community in rapidly flowing streams[3] and in waterfalls. Many members of the class are adapted to a planktonic existence. The phenomena of "water-bloom" and the "breaking of the meres"[4] are due to the sudden and often periodical appearance of large quantities of a few species of Myxophyceae, generally such as normally occur in the plankton. The extraordinary rapidity of their increase, which causes the discoloration of the water, together with their equally rapid disappearance, is not yet fully understood. Such occurrences appear however always to be associated with the presence of plentiful organic nutriment, whilst the sudden disappearance may be due to exhaustion of the available food-supplies or to the formation of toxic substances secreted by the organisms themselves[5]. Nelson[6] records that the presence of "water-bloom" often had a fatal effect on cattle which had been drinking the water[7].

With reference to the broad classification of the Myxophyceae there has been very little difference of opinion, saving as regards the position of a few genera. The arrangement here adopted is essentially the same as in the first edition, saving that Geitler has been followed in regarding the Chamaesiphonales as a group equivalent to the Chroococcales and Hormogoneales. Elenkin[8] has recently put forward a modified classification of the Chroococ-

[1] Murray, Phycol. Mem. III, 1895, p. 74.

[2] Seward, Fossil Plants, I, 1898, p. 125.

[3] cf. Geitler, Archiv f. Protistenkunde, LI, 1925, p. 321 et seq.

[4] cf. Phillips, Trans. Shrops. Archaeol. and Nat. Hist. Soc. VII, 1884, p. 277; see also Griffiths, Journ. Linn. Soc., Bot., XLVII, 1925, p. 90.

[5] cf. Kolkwitz, Ber. Deutsch. Bot. Ges. XXXII, 1914, p. 639; Naumann, Skrift. Södra Sverig. Fiskerifören. 1915, No. 13.

[6] Minnesota Bot. Studies, III, 1903, p. 52.

[7] Other Blue-green Algae also appear to be poisonous. West (1904, p. 316) reports, on the authority of Mr H. Wright, that numbers of horses have frequently been killed by feeding on *Lyngbya majuscula* Harvey, which occurs in abundance on the coral beaches in the Gulf of Mannar.

[8] Not. Syst. Inst. Crypt. Hort. Bot. Petropolitani, II, 1923, p. 65; cf. Rev. Algol. I, 1924, p. 69.

cales based essentially on the mode of arrangement of the cells in the colonies; in its general details this does not differ greatly from that adopted below. Few algologists will, however, be inclined to agree with him in the wholesale massing of genera which he advocates. A certain number of Blue-green Algae (*Glaucocystis*, *Gloeochaete*, *Chroothece*) have long presented difficulties because of the possession of well-differentiated chromatophores, and all kinds of systematic positions have been assigned to them. *Chroothece* has been dealt with at the end of the Rhodophyceae (p. 432), whilst the other two genera are placed as dubious forms at the conclusion of the consideration of the Myxophyceae proper. It is improbable that any of these genera are really members of the Myxophyceae.

The Blue-green Algae[1] are here classed in the following three groups:

I. *Chroococcales*, unicellular or colonial forms, commonly embedded in a gelatinous matrix, more rarely free-floating, without differentiation between base and apex (except in *Gomphosphaeria*), reproduction usually by simple division only.

II. *Chamaesiphonales*, unicellular or filamentous, always attached to some substratum, with differentiation between apex and base, reproduction commonly by means of gonidia, spores not recorded.

III. *Hormogoneales*, filamentous, with simple or branched filaments containing one or more trichomes within a sheath, reproduction largely by hormogonia, spores frequent in some families.

The following is a key to the British freshwater genera:

A. Cells without a properly differentiated chromatophore or nucleus (true Myxophyceae)

Group I. *Chroococcales*.

Cells or colonies free-floating or forming a gelatinous stratum, not epiphytic, reproduction by simple cell-division, very rarely by gonidia *Chroococcaceae*

a. Cell-division transverse to the long axis only, cells elongate, colonies without definite shape

1. Cells with rounded extremities

* Cells enveloped in mucilage

† Cells elongated, each with a distinct mucous coat *Gloeothece*

†† Cells little longer than broad, enveloped in a common mucous investment *Aphanothece*

** Cells destitute of mucus *Synechococcus*

[1] There are a number of very useful taxonomic works dealing with the Blue-green Algae as a whole, e.g. Lemmermann, 1910; Geitler, 1925; Tilden, Minnesota Algae, I, 1910. The last is however quite uncritical. See also Geitler, Beih. Bot. Centralbl. XLI, 1925, Abt. II, p. 163 et seq.

2. Cells with pointed extremities, enveloped in mucus *Dactylococcopsis*

b. Cell-division in two directions in one plane, colonies plate-like
1. Cells globular or rounded-quadrate, regularly arranged *Merismopedia*
2. Cells elongate, irregularly arranged, with the long axes vertical to the surface *Holopedium*
3. Cells commonly quadrate, often constricted, solitary or in small colonies *Tetrapedia*

c. Cell-division usually in all directions of space, cells enveloped in mucus, colonies with or without definite shape, but not plate-like
1. Cells forming large colonies
* Cells regularly grouped to form cubical colonies *Eucapsis*
** Cells arranged near the periphery of more or less spherical colonies
† Cells rounded or ovoid, colonies spherical, and hollow *Coelosphaerium*
†† Cells pyriform, ellipsoid, or spherical, at the ends of mucilage-stalks which radiate from the centre of the colony *Gomphosphaeria*
*** Cells densely aggregated in globose, elongate, or clathrate colonies *Microcystis*
**** Cells aggregated to form gelatinous colonies of no definite shape
† Individual mucous coats clearly evident round each cell *Gloeocapsa*
†† Cells embedded in a common mucilage envelope, without evident sheaths *Aphanocapsa*
2. Cells more or less solitary, or forming very small colonies *Chroococcus*

Group II. *Chamaesiphonales*.

Cells or filaments epiphytic, with a distinction between base and apex, reproduction mainly by gonidia.

a. Thallus composed of branched threads forming a creeping and upright system and densely compacted to form discs or cushions, often of large size, gonidia produced within sporangia *Pleurocapsaceae*
1. Upright threads few-celled, cell-membranes not gelatinising *Xenococcus*
2. Upright threads many-celled, cell-membranes of the inner cells gelatinising *Oncobyrsa*

b. Thallus composed of single, often elongate cells, with a firm sheath, gonidia formed apically by abstriction *Chamaesiphonaceae*
Only genus *Chamaesiphon*

Group III. *Hormogoneales.*

Plant composed of simple or branched filaments, reproduction by hormogonia

a. Trichomes cylindrical, sometimes narrowed at the extremities, unbranched or with false branches

1. Heterocysts absent, trichomes unbranched (except *Symploca*) *Oscillatoriaceae*

* Trichomes always singly within the sheath, when present *Lyngbyeae*

† Trichomes devoid of a sheath

§ Trichomes straight or with curved extremities *Oscillatoria*

§§ Trichomes twisted into a regular spiral

⊙ Without obvious septa *Spirulina*

⊙⊙ With obvious septa *Arthrospira*

†† Trichomes provided with a sheath

§ Sheaths thin, hyaline, more or less diffluent, trichomes agglutinated by their sheaths to form leathery, papery, etc. strata *Phormidium*

§§ Sheaths firm, sometimes coloured

⊙ Filaments free-floating or forming a matted stratum *Lyngbya*[1]

⊙⊙ Filaments forming erect tufts, often with solitary pseudo-branches *Symploca*

** Several trichomes within a single sheath, which is often branched *Vaginarieae*

† Sheaths always hyaline, not lamellose, with many trichomes *Microcoleus*

†† Sheaths often coloured, trichomes loosely aggregated within the sheath, not very numerous

§ Sheaths firm, lamellose, hyaline or coloured, with few or many trichomes *Schizothrix*

§§ Sheaths wide, hyaline or yellow-brown, diffluent, with very few trichomes *Dasygloea*

2. Heterocysts present, trichomes unbranched, sheaths gelatinous, not firm *Nostocaceae*

* Trichomes flexuous and contorted, within a definite gelatinous investment *Nostoc*

** Trichomes more or less straight, free, or forming a thin mucous stratum

† Heterocysts and spores intercalary

§ Trichomes nude or with a thin mucous sheath, free or aggregated without order to form a flocculent mass, cells equal to or longer than their diameter, spores solitary, geminate, or in short series *Anabaena*

[1] If with frequent geminate pseudo-branches, see *Plectonema* (Scytonemataceae, p. 481).

§§ Trichomes short, straight, aggregated in parallel bundles to form thin feathery plate-like masses *Aphanizomenon*

§§§ Trichomes free, spores seriate, remote from the heterocysts, cells shorter than their diameter *Nodularia*

†† Heterocysts terminal and the spores always contiguous to them *Cylindrospermum*

3. Heterocysts usually present, filaments mostly falsely branched, sheaths firm, including one or more trichomes *Scytonemataceae*

* Heterocysts absent, pseudo-branches often geminate *Plectonema*

** Heterocysts present

† One trichome within each sheath

§ Filaments simple, unbranched, heterocysts mainly basal, trichomes often somewhat attenuated *Microchaete*

§§ Filaments with frequent false branches

⊙ Branches often geminate, arising between the heterocysts *Scytonema*

⊙⊙ Branches usually single, adjacent to the heterocysts *Tolypothrix*

†† Two to six trichomes within each sheath

§ Filaments straight, trichomes with basal heterocysts *Desmonema*

§§ Filaments contorted, within a common sheath *Diplocolon*

b. Trichomes conspicuously attenuated towards one or both extremities which are generally piliferous, often falsely branched[1] *Rivulariaceae*

1. Trichomes attenuated from the base to the piliferous apex, heterocysts basal, rarely absent

* Heterocysts absent, filaments very narrow, forming a thin stratum *Amphithrix*

** Heterocysts usually present (absent in a few sp. of *Calothrix*)

† Filaments not united into a thallus of definite form

§ Filaments simple or falsely branched, branches distinct and free *Calothrix*

§§ Filaments falsely branched, several branches (2–8) within a common sheath[2] *Dichothrix*

†† Filaments radiately disposed within mucilage, forming a hemispherical or globular thallus

§ Thallus attached, globose or hemispherical, tough, spores unknown *Rivularia*

[1] cf. also *Microchaete*.

[2] cf. also *Desmonema*.

§§ Thallus attached or free-floating, globose, soft, spores regularly produced *Gloeotrichia*

2. Trichomes attenuated from the middle towards each extremity; heterocysts absent *Hammatoidea*

c. Filaments usually stout and showing true branching, trichomes often of more than one row of cells, heterocysts present, protoplasmic connections often distinct *Stigonemataceae*

1. Trichomes composed of a single row of cells *Hapalosiphon*

2. Trichomes composed of several rows of cells *Stigonema*

B. Cells with well-differentiated chromatophores and nuclei (*genera incertae sedis*)

a. Cells free-floating, solitary, or in twos, fours, or eights within the wall of the parent-cell *Glaucocystis*

b. Epiphytic, cells singly or in twos or fours, each with one or two long bristles *Gloeochaete*

GROUP 1. CHROOCOCCALES

Family 1. CHROOCOCCACEAE[1]

In this family are included the main mass of the unicellular and colonial Cyanophyceae[2]. The cells vary much in shape in the different genera and in the colonial forms are disposed in a variety of ways within the often extensive gelatinous investment. The latter is sometimes conspicuously lamellose, but more often it is hyaline and structureless. *Synechococcus* (fig. 183, D, E) and *Tetrapedia* (fig. 184, D) are the only genera which are commonly destitute of a mucous envelope. The protoplasts or the envelopes, as the case may be, often contain red, orange, or violet pigments. The normal method of multiplication is by simple cell-division, the larger colonies ultimately breaking up to form smaller ones. Sometimes young colonies arise at the sides of the older ones by a process of budding (fig. 185, A). Reproduction by gonidia or the formation of thick-walled spores is rare. The Chroococcaceae are abundant in all kinds of damp and wet situations, frequently forming a gelatinous stratum on the damp surfaces of dripping rocks; not a few are regular and abundant constituents of the freshwater plankton. None is epiphytic.

This family is badly in need of a critical revision. The generic

[1] cf. Crow, New Phytol. xxi, 1922, p. 81; Wille, Nyt Mag. f. Naturvidensk. lxii, 1924, p. 169.

[2] Geitler (1925, p. 120) has rightly separated the genus *Entophysalis* (not recorded for Great Britain) and one or two other forms, in which the cells show a tendency to an arrangement in rows attached to a substratum, from the rest of the Chroococcales.

differences are in part very slight and, whilst the more extreme forms are readily distinguished, groups of genera like *Gloeocapsa*, *Glocothece*, *Aphanocapsa*, *Aphanothece* no doubt grade over into one another. Innumerable species of these and other Chroococcaceous genera have been described, but many are very insecurely founded and in part no doubt mere habitat-forms of others. Very valuable work in the direction of clearing up some of the confusion has been done by Wille (loc. cit.), but this requires to be supplemented by observations such as those of Brand[1] on *Gloeocapsa alpina* and Brunnthaler[2] on *Gloeothece rupestris*. Till then, at least, the old-accustomed genera must be maintained; to abandon these at the present time would lead to chaos.

The species mentioned under the different genera in the following are probably in the main well established and represent forms that are frequently encountered in nature.

Gloeothece Naegeli, 1849[3]. Cells usually associated to form a small colony, elongated, ellipsoidal or cylindrical, each surrounded by a thick mucous coat which is sometimes faintly stratified; more rarely a number of cells embedded in a common mucilage-envelope. Cell-division always at right angles to the longit. axis of the cell; cells sometimes arranged with all the longitudinal axes more or less parallel to one another.

Sp. of this genus occur on wet rocks, among wet Mosses, and in bog-pools. Three or four Brit. sp. are known, the most frequent being *G. linearis* Naeg. (cells 10·5–18 l.; 1·3–2·3 br.) (fig. 183, A) and *G. confluens* Naeg. (cells 5·7–7·5 l.; 2·6–3 br.) (fig. 183, B).

Rhabdoderma lineare Schmidle and Lauterborn[4] would appear to be merely a form of *G. linearis* Naeg.

Aphanothece Naegeli, 1849[5]. Differs from *Gloeothece* only in the irregular and rather loose aggregation of large numbers of cylindrical, more or less elongated, cells within a common mass of mucilage to form usually large macroscopic strata.

Of the six Brit. sp., *A. microscopica* Naeg. (cells 5–8 l.; 3·5–4 br.) (fig. 183, C) and *A. saxicola* Naeg. are the most frequent, being found in bog-pools, at the margins of lakes, and on wet rocks; the latter sp. has pale-coloured strata and cells (1·5–1·8 br.; 2–3 times as long). *A. clathrata* W. & G. S. West, with small clathrate colonies of minute densely aggregated bacilliform cells (0·6–0·7 br.; 3·5–4·5 l.), is recorded

[1] Bot. Centralbl. LXXXIII, 1900, p. 224.
[2] Sitz.-ber. k. Akad. Wiss. Wien, Mat.-nat. Kl. CXVIII, 1909, p. 501.
[3] Naegeli, 1849, p. 57; Brunnthaler, loc. cit.
[4] Ber. Deutsch. Bot. Ges. XVIII, 1900, p. 148.
[5] Naegeli, 1849, p. 59.

from the plankton of various Irish lakes, whilst var. *endophytica* W. & G. S. West of *A. nidulans* P. Richter is a common endophyte in the colonies of *Coelosphaerium Kützingianum* (West and West, 1912, p. 432).

Fig. 183. A, *Gloeothece linearis* Naeg., from Old Cote Moor, W. Yorks. B, *G. confluens* Naeg., from near Settle, W. Yorks. C, *Aphanothece microscopica* Naeg., from Withiel, Cornwall. D and E, *Synechococcus aeruginosus* Naeg., from Adel Bog, W. Yorks. (All ×450.)

Synechococcus Naegeli, 1849[1]. Cells isolated or in short rows, often large, cylindrical, with hemispherical apices and a thin membrane, without a mucilage-envelope. Cell-contents usually brilliant blue-green, rarely rose-purple, with numerous large granules. Cell-division only at right angles to the longit. axis.

S. aeruginosus Naeg. (*S. major* Schroet., cells 26–29 l.; 15·5–17·5 br.) (fig. 183, D, E) is the most abundant sp., found free-floating in ponds and ditches, as well as in bog-pools. Several sp. are found on damp soil.

Dactylococcopsis Hansgirg, 1888[2]. Cells elongated, fusiform or lanceolate, with attenuated extremities, or sometimes sigmoidal, rarely solitary, generally collected to form small colonies which are often embedded in copious mucilage and are either free-floating or associated with other Algae. Pigmented zone of protoplast in some cases somewhat lateral in position. Cell-division transverse, sometimes faintly oblique.

[1] Naegeli, 1849, p. 56.

[2] Hansgirg, Notarisia, III, 1888, p. 590; and Prodr. d. Algenfl. v. Böhmen, II, 1892, p. 139.

There are two Brit. sp. *D. montana* W. & G. S. West (cells 8·6–11·5 l.; 3·5–4 br.) (fig. 184, A) occurs in bog-pools among *Sphagnum*, whilst *D. rhaphidioides* Hansg., with long spindle-shaped cells (5–25 l.; 1–3 br.), is known from the plankton of Lough Neagh.

Merismopedia Meyen, 1839[1]. Cells arranged in groups of four and in rectilinear series within structureless mucilage to form a flat 1-layered rectangular or irregular plate; cells globose, ellipsoidal, or oblong, sometimes slightly angular by compression, with homogeneous contents. Cell-division in two directions.

Of the four Brit. sp., *M. glauca* (Ehrenb.) Naeg. (cells 3·3–3·8 br.) (fig. 184, B) is the commonest, occurring in ponds, ditches, bogs, and

Fig. 184. A, *Dactylococcopsis montana* W. & G. S. West, from Widdale Fell, W. Yorks. B, *Merismopedia glauca* (Ehrenb.) Naeg., from Thursley Common, Surrey. C, *M. elegans* A. Br., part of a large colony from Wicken Fen, Cambridge. D, *Tetrapedia Reinschiana* Arch., from near Goring, Oxford. (All ×450.)

lakes, where it is often found in the plankton. *M. punctata* Meyen, with widely separated cells, and *M. elegans* A. Br. (*M. aeruginea* Bréb.), the largest sp. with deep blue-green cells (6·5–9·5 br.) (fig. 184, C), are not infrequent in stagnant water. The colonies of *M. glauca* and *M. elegans* often reach a large size (diam. up to 220 μ) and may contain as many as 1856 cells.

Holopedium Lagerheim, 1883 (incl. *Microcrocis* Richter, 1892)[2]. Cells cylindrical with rounded ends, irregularly disposed in 1-layered plate-like colonies in which the cells are placed with their long axes at right angles to the surface of the plate. Cell-division in two directions, parallel to the longitudinal axis of the cell.

[1] Naegeli, 1849, p. 55.

[2] Lagerheim, Öfvers. K. Sv. Vet.-Akad. Förhandl. XL, 1883, No. 2, p. 42; and Nuov. Notarisia, IV, 1893, p. 207.

H. irregulare Lagerh. (fig. 189, A) is reported by W. West from Clare Island, but this is so far the only Brit. record.

Tetrapedia Reinsch, 1867[1]. Cells in some sp. almost invariably solitary, but in others grouped in flat, 2–16 celled colonies like those of *Merismopedia*; cells flat, quadrate in general outline, often more or less constricted into two equal half-cells, with a firm wall and homogeneous contents. Cell-division in two directions along the lines of constriction.

The three Brit. sp. are all rare. *T. Reinschiana* Arch. (cells 5·5 -6 br.) (fig. 184, D) and *T. glaucescens* (Wittr.) Boldt (*Arthrodesmus glaucescens* Wittr.), with small spines at the corners of the cells (11 br.), occur in lakes and bog-pools. *T. setigera* Arch., which has been erroneously referred by some authors to *Tetraëdron*, is a beautiful sp. with triangular cells bearing long spines; it is known from N.W. Scotland and W. Ireland, as well as from the lake in the Royal Botanic Gardens, Kew.

Eucapsis Clements & Shantz, 1909[2]. Colonies usually of 32–128 spherical, or more rarely ellipsoidal, cells, arranged to form solid cubical free-floating packets. Cell-division along three directions at right angles to one another.

The genus differs essentially from *Merismopedia* only in the occurrence of division along three planes. *E. alpina* Clements & Shantz (diam. colon. 30–80; cells 6–7) (fig. 189, B) is recorded by W. West from Clare Island.

Coelosphaerium Naegeli, 1849[3]. Cells more or less closely grouped just within the periphery of a mass of mucilage (which sometimes shows faint radial striation) to form a hollow spherical

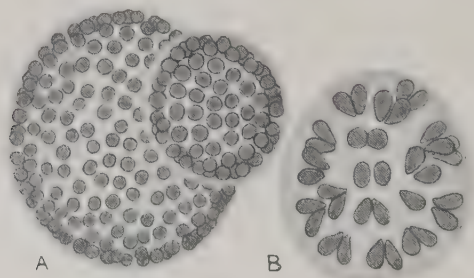

Fig. 185. A, *Coelosphaerium Kützingianum* Naeg., from the plankton of Lough Neagh, Ireland. B, *Gomphosphaeria aponina* Kütz., from Keston Common, Kent (×350).

[1] Reinsch, Algenfl. v. Franken, 1867, p. 37.
[2] Clements and Shantz, Minnesota Bot. Stud. IV, 1909, p. 133.
[3] Naegeli, 1849, p. 54; Bachmann, 1907, p. 60; Smith, 1920, p. 33.

colony; cells globose, ellipsoidal, or obovoid, with granular cell-contents, often including pseudo-vacuoles. Reprod. by division of colonies, by a kind of budding, and by liberation of single cells; cell-division along two directions at right angles to one another[1].

This genus is a common, and at times dominant, constituent of the freshwater plankton and is also found frequently in large ponds. The most abundant of the four Brit. sp. are *C. Kützingianum* Naeg. (colonies 48–90; cells 3–3·8 br.) (fig. 185, A) and *C. Naegelianum* Unger (*Gomphosphaeria Naegeliana* Lemm.); the latter has obovoid or ellipsoid cells (1·5–5 br.; 3·5–7 l.) with pseudo-vacuoles. *C. minutissimum* Lemm., with cells only 1 μ broad, is not uncommon.

Gomphosphaeria Kützing, 1836[2]. Cells grouped in pairs or fours towards the periphery of a globular or ellipsoid mass of mucilage, the cells situated at the ends of a system of short thick dichotomising mucilage-stalks which are formed from the split remnants of the parent cell-membranes and radiate from the centre: cells pyriform, obovoid, or ellipsoidal or, during their multiplication by longit. division, sometimes heart-shaped. Reprod. by splitting of colonies into two, and by the formation of gonidia.

Of the two Brit. sp., *G. aponina* Kütz. (colonies 64–78 br.; cells 8·5–11·5 l.) (fig. 185, B) is not uncommon in ponds, lakes, and stagnant ditches. *G. lacustris* Chod. (colonies 28–76 br.; cells 2–2·2 br.) (fig. 189, E) is a frequent constituent of the plankton of the Brit. lakes and may at times be a dominant form.

Crow[3] has advocated the inclusion of this genus in the Chamaesiphonales, owing to the usually obvious distinction of base and apex in the cells and the occurrence of gonidia. It must be borne in mind, however, that the mode of colony-formation is a widespread one (cf. *Dictyosphaerium*) and that, where so little is known of the reproduction, the possession of gonidia may not be as exceptional as it seems to be at present.

Microcystis Kützing, 1833[4]. (*Polycystis* Kützing, 1845; *Clathrocystis* Henfrey, 1856). Cells small, mostly globose, densely aggregated within structureless mucilage to form solid

[1] The principal difference between *Coelosphaerium* and *Gomphosphaeria* lies in the presence of mucilage-stalks, connecting the cells of the latter to a common centre. Troitzkaia (Not. Syst. Inst. Crypt. Hort. Bot. Petropolitani, II, 1923, p. 69; cf. Rev. Algol. I, 1924, p. 73), however, records the presence of stalks bearing the spherical cells of *C. Kützingianum*.

[2] Chodat, Bull. Herb. Boissier, VI, 1898, p. 180; Schmidle, Ber. Deutsch. Bot. Ges. XIX, 1901, p. 16; Geitler, loc. cit. p. 207.

[3] New Phytol. XXI, 1922, p. 86.

[4] Crow, ibid. XXII, 1923, p. 59.

colonies which may be spherical, ellipsoidal, oblong, much elongated, or clathrate; cell-contents blue-green, olive-green, or rose-purple in colour, often with pseudo-vacuoles. Cell-division in all directions.

There are about a dozen Brit. sp. *M. marginata* (Menegh.) Kütz. (cells 2·6 6 br.) (fig. 186, B), *M. flos-aquae* (Wittr.) Kirchn., *M. elabens* (Bréb.) Kütz., and *M. stagnalis* Lemm. (cells 1–1·5 br.) (fig. 186, A) are all common in bogs and lakes; all except *M. stagnalis* have pseudo-

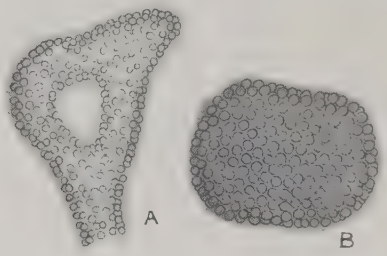

Fig. 186. A, *Microcystis stagnalis* Lemm., from the plankton of Lough Neagh, Ireland. B, *M. marginata* Menegh., from Old Cote Moor, W. Yorks (the margin of the mucilage-envelope is usually more distinct) (×450).

vacuoles, whilst *M. elabens* is one of the few sp. with elongate cells (1–1·5 br.; 3–5 l.). *M. aeruginosa* Kütz. (*Clathrocystis aeruginosa* Henfrey) (fig. 189, D) often occurs in prodigious quantity in ponds and in the plankton of lakes. *M. stagnalis* Lemm. and *M. incerta* Lemm. are other common planktonic sp.

M. roseo-persicinus Kütz. (*Clathrocystis roseo-persicina* Cohn), which is often found abundantly in ponds and ditches containing much decaying vegetation, is a Schizomycete.

Gloeocapsa Kützing, 1843; emend. Naegeli, 1849[1]. Cells globose, embedded in groups of 2–32 within stratified mucilage-sheaths which represent the envelopes of successive generations and may be colourless, yellow, brown, blue, violet, or red, innumerable such groups being usually combined to form large irregular expanses constituting gelatinous crusts or strata[2]. Cell-division alternately along three planes at right angles to one another, the products becoming irregularly arranged; at times more irregular divisions occur. Thick-walled resting spores known in some sp. (*G. alpina*, *G. gigas*, *G. sanguinea*).

[1] Brand, loc. cit. 1900; Wille, Vidensk. Selsk. Skrift. 1906, No. 3, p. 21, and loc. cit. p. 184. Various authorities identify *Bichatia* Turpin, 1827, with *Gloeocapsa*, but G. S. West (1904, p. 350) was of the opinion that this was uncertain.

[2] Within the interior of such strata the sheaths of the various groups may become diffluent and combine to form a homogeneous mass of mucilage.

There are about 20 Brit. sp., some of which are of doubtful validity. Most occur on wet or dripping rocks, generally associated with other Myxophyceae. *G. punctata* Naeg. (cells 1·5–2 br.) is the smallest, forming blackish or greenish-grey strata. *G. polydermatica* Kütz. is remarkable for the lamellation of the envelopes (fig. 187, C–E). *G. magma* (Bréb.) Kütz., with golden-yellow or brown envelopes (fig. 187, B), and *G. Ralfsii* (Harv.) Lemm. (*G. Ralfsiana* Kütz.), with bright red or purple envelopes, are two of the best-defined sp.; the former is very abundant in W. Scotland and the Hebrides in the form of lobed, brownish-purple patches found among stones on wet ground and locally known as "mountain dulse." Sp. of this genus are the algal constituents of some Lichens.

Aphanocapsa Naegeli, 1849[1]. Cells globose, blue-green or olive-green in colour, mostly without individual mucilage-sheaths, irregularly and loosely aggregated to form smaller or larger colonies within a common homogeneous mass of mucilage

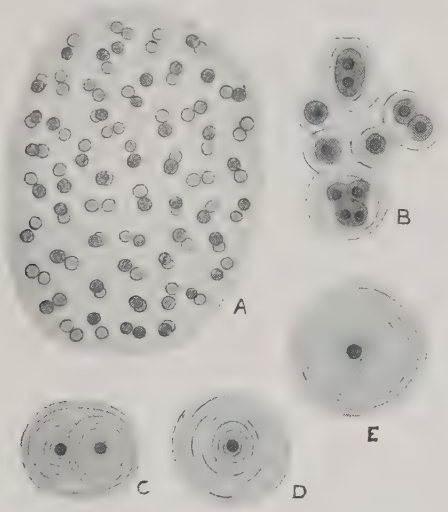

Fig. 187. A, *Aphanocapsa Grevillei* (Hass.) Rabenh., from Helln Pot, W. Yorks. B, *Gloeocapsa magma* (Bréb.) Kütz., and C–E, *G. polydermatica* Kütz., both from Boston Spa, W. Yorks. (All × 450.)

which may be colourless, brown, or blue-green. Cell-division in all directions[2]. The genus only differs from *Aphanothece* in the shape of the cells, and from *Microcystis* in their less dense aggregation.

[1] Naegeli, 1849, p. 52.

[2] According to Geitler, 1925, p. 63, division often takes place only along one plane, the daughter-cells becoming displaced in all directions.

There are six Brit. sp. Some are found in stagnant water or covering wet rocks with extensive gelatinous strata, whilst others occur in the plankton. The most frequent sp. is *A. Grevillei* (Hass.) Rabenh. (cells 3·4–4·5 br.) (fig. 187, A). A characteristic plankton-form is *A. delicatissima* W. & G. S. West, with more or less ellipsoidal colonies containing very minute cells (0·5–0·75 br.).

Chroococcus Naegeli, 1849[1]. Cells globose, solitary or associated in small colonies of 2–4–8–16 or more cells which are free-floating or mixed with other Blue-green Algae to form a stratum on wet rocks; mucilage-envelopes about the individual cells or cell-groups firm, narrow or wide, homogeneous or lamellated, generally colourless, but sometimes yellowish-brown; cell-

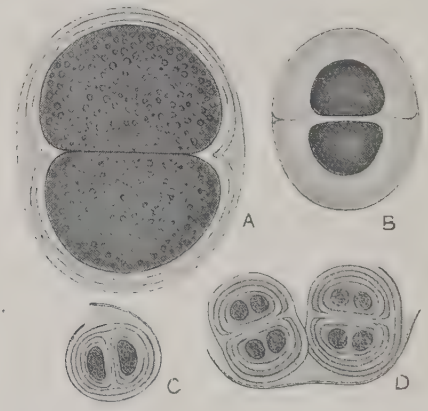

Fig. 188. A, *Chroococcus giganteus* West, from Bowness, Westmorland. B, *C. turgidus* (Kütz.) Naeg., from Slieve Donard, Down, Ireland. C and D, *C. schizodermaticus* West, from near Windermere, Westmorland. (All ×450.)

contents granular, brilliant blue-green or more rarely brown, violet, olive-green, or yellow-green. Cell-division along three planes at right angles to one another. Gonidia recorded in one sp.[2] A genus closely related to *Gloeocapsa*, which differs principally in the formation of much larger colonies and the more irregular arrangement of the cells.

There are about ten Brit. sp., of which the most widely distributed is *C. turgidus* (Kütz.) Naeg. (cells 13–25 br.) (fig. 188, B), which often occurs in quantity in *Sphagnum*-bogs and is also frequent in salt-marshes. *C. cohaerens* (Bréb.) Naeg., *C. giganteus* West (fig. 188, A), *C. minor* (Kütz.) Naeg., and *C. pallidus* Naeg. are not infrequent in

[1] Naegeli, 1849, p. 45; Acton, loc. cit. p. 438; Wille, loc. cit. p 172.
[2] West, 1916 *a*, p. 25.

ponds, lakes, and bog-pools; all of these except *C. giganteus*, which is characterised by its huge cells (54–58 br.), form extensive strata. *C. schizodermaticus* West (fig. 188. C and D) is remarkable for its tough stratified envelopes, the layers of which are gradually split off and shed. *C. limneticus* Lemm. is a frequent constituent of the Brit. plankton.

Another not uncommon form in the bogs of moorland and upland districts is *C. macrococcus* Rabenh. (*Urococcus insignis* (Hass.) Kütz.; *Haematococcus insignis* Hass.) which sometimes occurs abundantly amongst submerged *Sphagnum*, especially in peaty pools; the cell-contents are golden to dark brown and the envelope is thick and lamellose, the outer layers often splitting off; cells 25–51 br., with integument 41–78 br. Acton (loc. cit. p. 448) has expressed the opinion that *Chroothece Richterianum* Hansg. (cf. p. 433) is but a form of this long misunderstood sp.

GROUP 2. CHAMAESIPHONALES

Family 1. PLEUROCAPSACEAE

The members of this family, as Geitler[1] was the first to expound clearly, possess a branched filamentous thallus differentiated into an attaching base and a more or less well-marked upright system (cf. Chaetophorales among the Isokontae), both exhibiting apical growth; the base is often parenchymatous, through coalescence of filaments. The upright system usually consists of densely aggregated threads which are either placed vertically (*Pleurocapsa*) or exhibit a radial arrangement (*Oncobyrsa*), thus giving rise to crusts, or more or less hemispherical cushions, as the case may be. In some genera (*Oncobyrsa* (fig. 189, K)) the cells in the inner parts of the cushion exhibit marked gelatinisation of the membranes, so that the filamentous habit is obscured and a colonial one is suggested. Reproduction takes place by the formation of gonidia (Geitler's endospores) within enlarged cells (sporangia) which are often terminal.

The relationships of this rather specialised group of forms, which are apparently better represented in the sea, are altogether obscure. It may be doubted whether there is any close affinity with *Chamaesiphon*. The majority of the freshwater forms occur as epiphytes on stones and larger Algae in rapidly flowing waters. Few are at present known from the British Isles.

Xenococcus Thuret, 1875; emend. Geitler, 1925[2]. Thallus composed only of a parenchymatous basal disc, or of the latter together with numerous relatively short, few-celled, upright threads coalescing laterally to form a more or less extensive

[1] Geitler, Archiv f. Protistenkunde, li, 1925, p. 343, and Beih. Bot. Centralbl. xli, 1925, Abt. ii, p. 238; also Geitler, 1925, p. 124.

[2] cf. Geitler, Archiv f. Protistenkunde, li, 1925, p. 348.

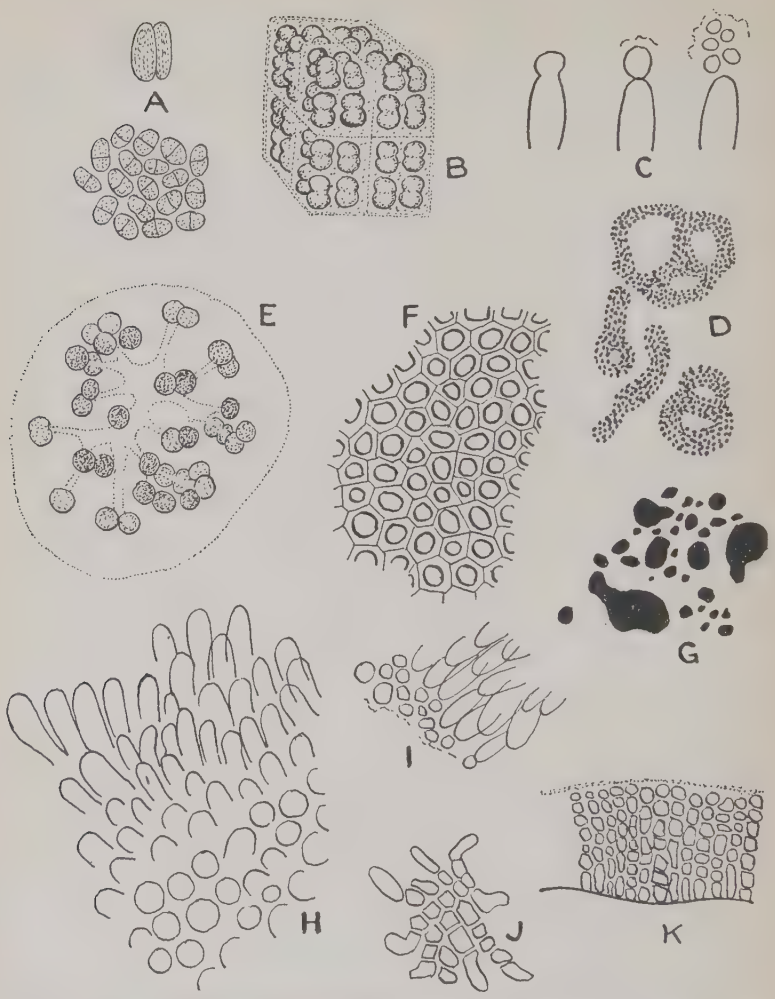

Fig. 189. A, *Holopedium irregulare* Lagerh. (after Lagerheim, ×480); the two upper cells seen from the side, the lower ones in surface-view. B, *Eucapsis alpina* Clements & Shantz (after Clements & Shantz). D, *Microcystis aeruginosa* Kütz. (after Kirchner, ×24). E, *Gomphosphaeria lacustris* Chod. (after G. M. Smith, ×825). C and F–I, *Xenococcus britannica* n.sp., from the East Lyn, Devonshire; F, basal layer; G, a number of the strata (nat. size); and H, superficial layer of stratum; C and I show formation of gonidia (×480). J–K, *Oncobyrsa rivularis* Kütz. emend. Geitler (after Geitler, ×800); J, prostrate threads of juvenile stages; K, vertical section of young stratum.

parenchymatous stratum. Cell-membranes delicate or thickened, not gelatinising. Reprod. by gonidia formed in sporangia which are either produced at the margin of the basal stratum, or at the ends of the upright threads; in some cases also formed by abstriction from the marginal cells (?).

X. britannica n.sp. (*Oncobyrsa britannica* Fritsch[1]) (fig. 189, C, F–I) is a very abundant form on the pebbles in the beds of many Devonshire streams and will no doubt be found in other parts of the country; it forms small roughly circular patches or large irregular incrustations of a brownish-black or sometimes faintly purple colour. *X. rivularis* (Hansg.) Geitler (*Pleurocapsa rivularis* Hansg., cells 3–4 br.) has been found attached to *Cladophora* in Devonshire streams; in this sp. only the creeping base is known.

Oncobyrsa C. A. Agardh, 1827[2]. Thallus composed of basal disc and upright densely packed threads, forming extensive strata; upright threads comprising numerous cells, whose membranes become gelatinous in the inner parts of the stratum and give rise to an amorphous mass of mucilage within which the cells appear embedded. Sporangia and gonidia unknown.

O. rivularis Kütz. emend. Geitler (cells of upright threads 1·5–3·5 br.) (fig. 189, J, K) forms small colonies attached to rocks and other Algae in the Devonshire streams.

Family 2. CHAMAESIPHONACEAE

This includes only the genus

Chamaesiphon A. Braun & Grunow, 1864[3] (incl. *Sphaerogonium* Rostafinski, 1883). Unicellular, epiphytic on other aquatics, usually aggregated in dense clusters, sometimes

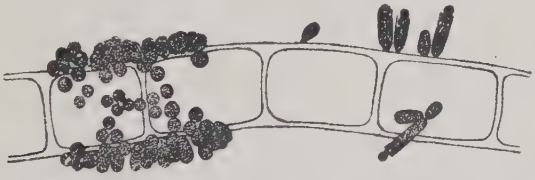

Fig. 190. *Chamaesiphon incrustans* Grun., on a filament of *Rhizoclonium*, from Heaton, W. Yorks (×416).

colonial; cells small, ovoid, pyriform, cylindrical, or much elongated (many times as long as broad), often widening from the base upwards; membrane thin; cell-contents homogeneous,

[1] Journ. of Ecol. XIII, 1925, p. 173.
[2] Geitler, loc. cit. p. 350.
[3] cf. Geitler, loc. cit. p. 322.

blue-green, violet, or yellow in colour. No vegetative cell-division. Reprod. by gonidia abstricted successively from the upper end of the protoplast which is exposed by the membrane rupturing apically; the ruptured membrane appears as an open sheath around the protoplast.

The affinities of *Chamaesiphon* are altogether obscure. It is possible that the peculiar mode of gonidium-formation is derived from that of the Pleurocapsaceae. Geitler (loc. cit.) has recently described an interesting colonial species (*C. fuscus* Hansg.) in which *Dinobryon*-like groupings are produced by germination of the gonidia at the mouth of the ruptured membrane; in other species (e.g. *C. polymorphus* Geitler) the abstricted gonidia are kept *in situ* by excreted mucilage and, since they in their turn form gonidia, long chains of cells may arise simulating a filamentous construction.

Only three Brit. freshwater sp. have so far been recorded. Of these, *C. confervicola* A. Br. occurs as an epiphyte on *Cladophora*, *Rhizoclonium*, *Vaucheria*, etc., whilst *C. incrustans* Grun. (cells 3·5—4·8 br.) (fig. 190) often thickly covers filaments of *Rhizoclonium* and *Oedogonium*. The former differs from the latter in the enlargement of the apex of the reproductive cell and the production of more numerous gonidia.

GROUP 3. HORMOGONEALES[1]

Family 1. OSCILLATORIACEAE

This includes the simpler non-heterocystous members of the Hormogoneales. The trichomes consist of a uniform row of often very short, discoid cells, and are either straight or flexuose, rarely spirally twisted (fig. 192). They are devoid of a special sheath only in a few genera (*Oscillatoria*, *Spirulina*). They either float freely or form a more or less firm mucilaginous stratum on damp surfaces, submerged stones, or on the muddy bottom of ponds and ditches.

Generic differences are mainly based on the characters of the sheath, as well as on the number (one to many) of trichomes included within it. Specific differences depend *inter alia* largely on the features presented by the apices of the trichomes[2], which

[1] Some authorities distinguish within this group the Psilonemateae (Oscillatoriaceae, Nostocaceae, Scytonemataceae, Stigonemataceae) and Trichophoreae (Rivulariaceae, Camptotrichaceae, see p. 491)—the latter characterised by the conspicuous attenuation of the trichomes towards one or both extremities, which are generally piliferous. This lays too much stress on a minor character.

[2] As a general rule only a certain number of the trichomes in a stratum show the typical apex.

are sometimes slightly attenuated. The apical cell may be rounded, conical, or more or less dilated (capitate) (fig. 191, A), and its external surface is frequently covered by a slightly thickened hood (the *calyptra*) (cf. fig. 191, B, C); it is probable that the latter is of diverse nature, sometimes representing a thickening of the membrane, in other cases a collapsed terminal cell[1]. The trichomes are often perfectly cylindrical with straight margins, but in other species there may be a more or less pronounced constriction between the cells. Several of the Oscillatoriaceae exhibit slow gliding or rotatory movements (p. 447). Reproduction is mainly effected by hormogonia. With reference to the occurrence of spores, cf. Brand (loc. cit. 1903, p. 37) and Hansgirg (loc. cit. p. 75).

The Oscillatoriaceae have been well monographed by Gomont[2] and, though some of the specific differences employed appear a little unsatisfactory, the taxonomy is better founded than that of any other family of Blue-green Algae. They are usually subdivided into

Sub-family 1. *Lyngbyeae*, in which there is only one trichome within the sheath, when the latter is present[3].

Sub-family 2. *Vaginarieae*, in which several trichomes are included within a common sheath which is frequently branched.

Sub-family 1. Lyngbyeae

Oscillatoria Vaucher, 1803[4] (*Oscillaria* Bosc, 1800)[5]. Trichomes free or interwoven to form a thin stratum, cylindrical, devoid of a sheath (in rare cases with a temporary sheath, e.g. *O. Agardhii* Gom.)[6], the edges usually presenting a continuous unbroken line, though faint constrictions are evident between the cells in some sp.; cells varying much in the relation of length to breadth, but in the wider sp. always very short and discoid, septa in some sp. obscured by rows of fine granules. Extremity of trichome straight or curved and often attenuated; apical cell sometimes rounded, sometimes much attenuated or capitate (fig. 191, A), frequently furnished with a calyptra. For move-

[1] Brand, Hedwigia, XLV, 1906, p. 9.

[2] Ann. sci. nat., Bot., sér. 7, XV, 1892, p. 263, and XVI, 1892, p. 91.

[3] The genus *Plectonema*, which is often referred to Oscillatoriaceae, is probably better regarded as a non-heterocystous member of the Scytonemataceae (p. 481).

[4] Schmid, Jahrb. Wiss. Bot. LX, 1921, p. 572; Funk, Ber. Deutsch. Bot. Ges. XXXVIII, 1920, p. 267.

[5] For reasons for adopting the generic name "*Oscillatoria*" see Gomont, Journ. de Bot. V, 1891, p. 273.

[6] Lemmermann, Arch. f. Hydrobiol. u. Planktonk. IV, 1909, p. 181.

ments of the trichomes, see p. 447. Gonidia known in a few sp. (cf. Lemmermann, 1910, p. 18).

Sp. of this genus are met with in great profusion in all kinds of wet situations, as well as on damp ground. Flocculent masses of *Oscillatoria*, intermixed with a certain amount of mud, are often found floating on the surfaces of ponds and ditches after sunshine; these are portions of the stratum covering the bottom, which float owing to the retention of bubbles of oxygen amongst the intricate network of trichomes. They commonly give off a more or less distinctive odour.

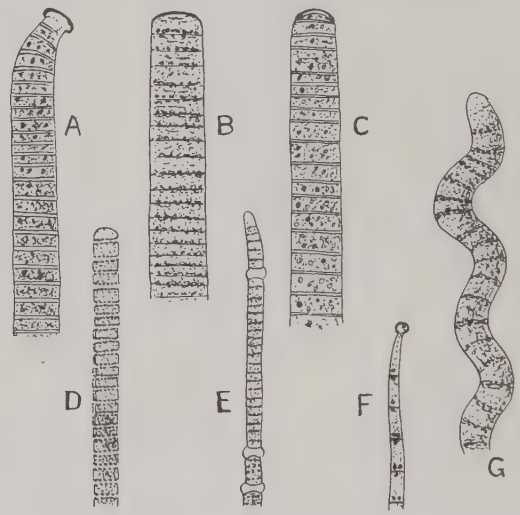

Fig. 191. A, *Oscillatoria proboscidea* Gom. B, *O. limosa* Ag. C, *O. irrigua* Kütz. D, *O. tenuis* Ag. E, *O. brevis* Kütz. F, *O. splendida* Grev. G, *Arthrospira Jenneri* Stiz. (All after Gomont, F × 875, the remainder × 520.)

There are about 20 Brit. sp., one of which (*O. decolorata* G. S. West, 1899, p. 263) is destitute of pigment and leads a saprophytic existence in stagnant ditches. *O. princeps* Vauch., with attenuated apices and a slightly capitate apical cell, is the largest (trich. 25–50 br.) and *O. angustissima* W. & G. S. West, whose cells are up to twice as long as broad, the narrowest (trich. 0·6 br.). The most abundant are *O. limosa* Ag. (trich. 12–17 br.) (fig. 191, B) and *O. tenuis* Ag. (4–10 br.) (fig. 191, D). *O. irrigua* Kütz. (fig. 191, C) is common in quickly running water; the apical cell has a somewhat thickened membrane. *O. rubescens* DC. is a characteristic plankton-sp. which is found in the Brit. Isles, forming purplish floating masses; the apical cell is capitate with a well-marked calyptra.

Spirulina Turpin, 1827[1]. Trichomes very narrow, twisted into a regular spiral, the coils being far apart or closely arranged; septa indistinct or absent. Regarding movements, see p. 447.

Fig. 192. A, *Spirulina turfosa* Cram., from Lough Neagh, Ireland. B, *S. major* Kütz., from Wicken Fen, Cambridge (×480).

According to Schmid (loc. cit.) septa are readily brought to light by staining with neutral red and in some sp. are indicated by granules located on either side of the wall. On the strength of this observation, Geitler (1925, p. 342) includes *Arthrospira* (cf. below) in the genus *Spirulina*. There can be no doubt that septa occur in some, though perhaps not in all, sp. of the latter genus. The habit of the sp. of *Spirulina* is however so distinctive that a separate genus appears warranted on that score alone, quite apart from the usual obscurity of any septation.

There are three Brit. sp. *S. major* Kütz. (trich. 1·5–2·5 br.) (fig. 192, B) is frequent in stagnant water and *S. tenuissima* Kütz. (*S. subsalsa* Oersted) is often abundant in salt and brackish water, rarely occurring in freshwater; the trichomes (1–2 br.) in the latter are twisted into a close spiral.

Arthrospira Stizenberger, 1852. Trichomes of moderate width, cylindrical, devoid of a sheath, twisted into a regular spiral; cells generally shorter than their diam., with well-marked septa. Regarding movements, see p. 447.

A. Jenneri Stiz. (fig. 191, G) occurs rarely in stagnant water or forms a dark green mucous stratum in trickling water; trich. 5–8, coils of spiral 9–15 br.

With reference to the relation of this genus to *Spirulina*, see under the latter.

Phormidium Kützing, 1843 (*Hypheothrix* Kützing, 1843 (in part); *Leptothrix* Kützing, 1843 (in part)). Filaments[2] sometimes subparallel but more commonly densely interwoven, usually agglutinated to form extensive foliaceous strata which are often soft and slimy, but in some sp. papery, leathery, or even subcartilaginous; sheaths delicate, hyaline, frequently becoming confluent or altogether diffluent, in some sp. giving a blue coloration with chlor-zinc-iodide. Trichomes cylindrical, with straight or curved apices, in some sp. with prominent constriction between the cells, so that the threads appear moniliform or torulose; apical cell attenuated or capitate, sometimes with a calyptra. Gonidia known in a few sp.

Sp. of this genus are amongst the commonest Blue-green Algae, the strata occurring either on damp earth, wet rocks, or entirely

[1] Schmid, Archiv f. Protistenk. XLIII, 1921, p. 463.

[2] i.e. sheath + contained trichome, cf. footnote on p. 436.

submerged. They often give a decided tint to large areas of damp ground or vertical limestone rocks, and are very characteristic features on rocks in waterfalls and rapidly flowing streams. There are about 13 Brit. sp. *P. autumnale* (Ag.) Gom., with trichomes (4–7 br.) usually having a well-marked capitate apical cell, is abundant on damp earth, whilst *P. tenue* (Menegh.) Gom. (trich. 1–2 br.) (fig. 193, E, F), with thin membranous strata, is frequent among other Algae in ponds, ditches, and rivers; the filaments of both sp. are also commonly encountered in cultivated soils (Bristol, 1920, p. 44). *P. purpurascens* (Kütz.) Gom. (trich. 1·5–2 br.) forms reddish-purple leathery patches on the vertical faces of wet limestone rocks. *P. Retzii* (Ag.) Gom., with large blue-green to slate-green strata, is an abundant form in rapidly flowing water[1].

Lyngbya C. Agardh, 1824 (*Leibleinia* Endlicher, 1836; *Leptothrix* Kützing, 1843 (in part); *Spirocoleus* Möbius, 1889 (in part)). Filaments free-floating or densely intertwined to form a floccose mass or an expanded stratum; sheaths firm, of variable thickness, sometimes lamellose, generally hyaline, but in a few

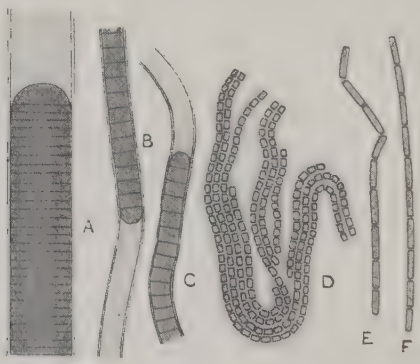

Fig. 193. A, *Lyngbya major* Menegh., from Wimpole Park, Cambridge. B and C, *L. aerugineo-coerulea* (Kütz.) Gom., from Bradford, W. Yorks. D, *Phormidium molle* (Kütz.) Gom. (a narrow form), from Bradford, W. Yorks. E and F, *P. tenue* (Menegh.) Gom., from Wicken Fen, Cambridge. (All ×460.)

sp. becoming yellow-brown in later stages. Trichomes obtuse or slightly attenuated at the apices, sometimes with evident constrictions between the cells. Gonidia known in one sp. (p. 449).

Sp. of this genus are widely distributed and occur in very varied habitats. A number of sp., largely marine, grouped in the subgenus

[1] *Clonothrix gracillima* W. & G. S. West is a species of *Cladothrix* (Schizomycetes).

Leibleinia, are attached to larger Algae or are found on pebbles in streams; these epiphytic forms are as yet very imperfectly known.

Of the 12 Brit. freshwater sp., *L. Martensiana* Menegh., with rather thick structureless sheaths (trich. 6–10 br.), and *L. aerugineo-coerulea* (Kütz.) Gom. (trich. 4–6 br.) (fig. 193, B and C) are the most abundant. *L. ochracea* (Kütz.) Thur.[1] occurs in water containing much iron, the oxide of iron ultimately forming a thick deposit round the sheaths of the filaments. *L. aestuarii* (Mert.) Liebm. is the largest Brit. freshwater sp. (trich. up to 24 br.), although it is principally found in brackish or marine habitats; the sheaths of old filaments are yellow-brown and stratified. Several sp. of *Lyngbya* occur in the freshwater plankton (cf. West and West, 1909 *a*, p. 187), and of these some have spirally twisted filaments (e.g. *L. contorta* Lemm., which is known from the Scotch lakes).

Note. The genera *Oscillatoria*, *Phormidium*, and *Lyngbya*, whilst closely allied, are readily distinguished. The strata occasionally formed by the first and last are easily seen, sometimes even with a lens, to possess a filamentous texture, whilst those of *Phormidium* are far more compact, since the component filaments are agglutinated by a basis of mucilage. The trichomes of all three are sometimes found separate[2].

Symploca Kützing, 1843. Filaments densely interwoven to form a creeping stratum giving rise to numerous erect tufts of variable height (fig. 194, B); filaments in some sp. with pseudobranches arising singly; sheaths thin, hyaline, and generally firm, partially coalescent in the erect tufts. Trichomes with straight apices.

S. muralis Kütz. occurs on damp earth, walls, or trunks of trees; it is known from W. Yorkshire and Wyre forest (trich. 3·4–4 br.) (fig. 194, B, C). *S. thermalis* Kütz. (trich. 1·2–2 br.; cells 2–3 times as long as broad) is found growing in chinks between the brickwork of the pits in the Royal Botanic Gardens, Kew (Fritsch, 1906, p. 212). Other sp. occur among Mosses and dead leaves and some are found in hot springs.

Sub-family 2. Vaginarieae

Microcoleus Desmazières, 1823 (*Chthonoblastus* Kützing, 1843). Filaments rather coarse, simple or sparsely branched, terrestr. or aquat., furnished with a conspicuous, wide, hyaline,

[1] This species is probably one of the Bacteria (*Chlamydothrix ochracea* (Kütz.) Mig.); cf. Naumann, Arkiv f. Bot. xvi, 1919, No. 1, p. 10; Grove, 1920, p. 7.

[2] A key for the determination of such isolated trichomes has been prepared by Wager (Naturalist, 1913, p. 305 et seq.). The determination of species without knowing the characteristics of the stratum is, however, scarcely to be advocated.

more or less cylindrical, non-lamellose sheath, generally diffluent at the apex. Trichomes numerous, closely aggregated within the central part of the sheath, often densely interwoven; apical cell acute or acutely conical, rarely capitate.

Sp. of this genus are not common in Britain. *M. vaginatus* (Vauch.) Gom., with conical capitate end-cells to the trichomes (3·5–7 br.), is occasionally found on damp ground, whilst *M. Chthonoplastes* Thur., in which the trichomes show constrictions between the cells and the end-cell is not capitate, is a frequent member of salt-marsh floras. *M. subtorulosus* (Bréb.) Gom. (trich. 4–5 br.) and *M. delicatulus* W. & G. S. West (trich. 1·5–2 br.) (fig. 194, A) are known from Scotland.

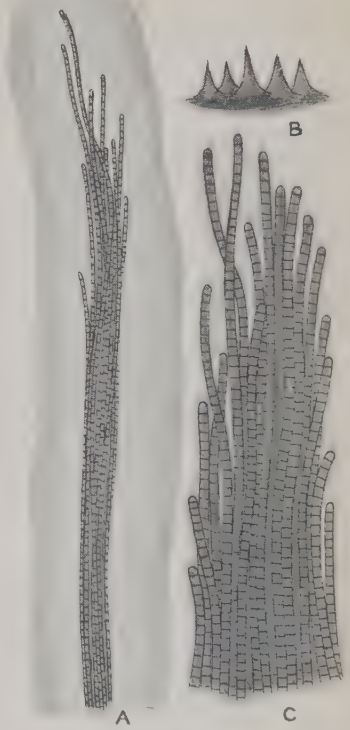

Fig. 194. A, *Microcoleus delicatulus* W. & G. S. West, from Glen Tummel, Perthshire (×350). B and C, *Symploca muralis* Kütz., from Frizinghall, W. Yorks (B, nat. size; C, ×350).

Schizothrix Kützing, 1843 (incl. *Inactis* Kützing, 1843; *Hypheothrix* Kützing, 1843 (in part)). Filaments occasionally floating freely in water (*Inactis*), more usually agglomerated to form small cushion-like masses (*Inactis*), erect tufts (*Symplocastrum*), or a flat stratum (*Hypheothrix*), sometimes impregnated with lime; filaments simple or variously branched, occasionally of great length; sheaths firm, close-fitting, or wide and more or less lamellose, generally attenuated towards the apex, not uncommonly coloured (esp. section *Chromosiphon*), the inner layers being any shade of yellow, yellow-brown, purple, or blue and usually of a deeper tint than the outer layers. Trichomes relatively few (sometimes only one) within each sheath, laxly disposed, and sometimes interwoven.

The numerous sp. are grouped in the four sections above mentioned, which are distinguished by the habit and the coloration of the sheaths. The genus is not very sharply marked off from *Microcoleus*, but is

characterised by its lamellose and often coloured sheaths and the fewer less densely aggregated trichomes. Of the six Brit. sp., the largest is *S. Muelleri* Naeg., with golden-yellow sheaths (trich. 7–13 br.) (fig. 195, A), and the smallest *S. delicatissima* W. & G. S. West (trich. 0·6–0·8 br., with conical apical cells); both are found on damp earth and the former also in stagnant water. *S. calcicola* (Ag.) Gom.

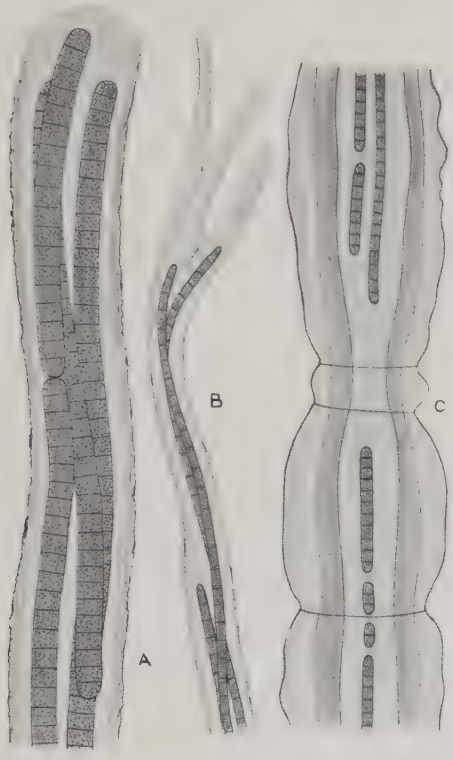

Fig. 195. A, *Schizothrix Muelleri* Naeg., from Penyghent, W. Yorks. B, *S. lardacea* (Ces.) Gom., from Arncliffe, W. Yorks. C, *Dasygloea amorpha* Berk. (a small form), from Thursley Common, Surrey. (All ×460.)

(trich. 1–1·7 br.) and *S. lardacea* (Ces.) Gom. (fig. 195, B) are not infrequent on wet rocks. In *S. funalis* W. & G. S. West, another very small sp. (trich. 0·5–0·7 br.), the branches of the filaments are twisted round each other like the strands of a rope. *S. fasciculata* (Naeg.) Gom. is responsible for the formation of spherical calcareous pebbles on the bottom of Lough Belvedere, near Mullingar, Ireland.

Dasygloea Thwaites, 1848. Differs principally from *Schizothrix* in the possession of relatively wider sheaths enclosing few remotely placed trichomes.

D. amorpha Berk. (trich. 4–6 br.) (fig. 195, C) forms a mucilaginous stratum in permanent bogs.

Family 2. NOSTOCACEAE

These, the simplest of the heterocystous Hormogoneales, are characterised by the unbranched filaments which are never fixed by one extremity. The trichomes consist of a single series[1] of uniform, often torulose, cells; they may be straight and rigid (*Aphanizomenon*) (fig. 198, A), but are often contorted and sometimes form densely interwoven masses (*Nostoc*) (fig. 196). The heterocysts are terminal or intercalary. The sheaths are thin and very mucilaginous, being relatively distinct and closely investing the trichomes in some cases (cf. *Nodularia*) (fig. 197, H), but in others they flow together to form a watery mass of jelly enclosing a large number of trichomes. In *Nostoc* this gelatinous mass becomes most conspicuous and usually has a tough bounding layer. Whenever there is a fracture of a filament, trichome and sheath both break at the same point, and empty sheaths, such as are commonly found in Scytonemataceae and Stigonemataceae, do not occur in this family.

Reproduction takes place by hormogones and spores. The former are produced by the fragmentation of fully grown trichomes and, where necessary, are set free by the dissolution of the enveloping mucilage[2]. The spherical, ellipsoidal, or cylindrical spores often arise in relation to the heterocysts (fig. 197) and may be developed singly or in series. Since they are of regular occurrence, their shape and position furnish the chief characters for the discrimination of genera and species.

About half the species of *Nostoc* and *Cylindrospermum* are terrestrial, but all the other members of the family are aquatic; many species of *Anabaena* are characteristic of the freshwater plankton. Certain species of *Nostoc* and *Anabaena* are endophytes in higher plants (*Anthoceros*, *Sphagnum*, *Azolla*, *Cycas*, *Lemna*, etc.), whilst other species of *Nostoc* are constituents of various Lichens, especially of the Collemaceae. Species of *Nostoc* are used as food by the inhabitants in diverse parts of the world.

[1] In young colonies, arising from germinating spores or hormogones, a false impression of a biseriate arrangement is sometimes given (cf. fig. 182, I).

[2] With reference to their movements, see Harder, Zeitschr. f. Bot. x, 1918, p. 177.

The heterocystous Myxophyceae have been excellently monographed by Bornet and Flahault[1].

Nostoc Vaucher, 1803[2]. Thallus terrestr. or aquat., sometimes attached to a substratum, at other times floating freely, composed of a more or less firm jelly with a denser limiting layer, within which are innumerable contorted moniliform trichomes; thallus at first almost always globose or ellipsoidal; when mature, either retaining this shape, being solid or hollow and varying in diam. from 1 or 2 mm. to several cms., or more frequently breaking open to form extensive flattened expansions, often with lacerated margins. Trichomes much contorted,

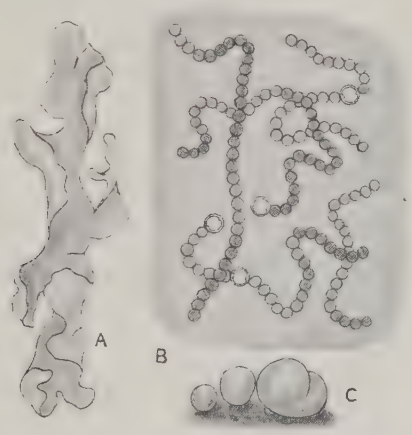

Fig. 196. A and B, *Nostoc Linckia* Bornet, from Ben Lawers, Perthshire; A, nat. size; B, small portion of thallus, ×340. C, *N. coeruleum* Lyngb., from R. Wharfe at Ilkley, W. Yorks., nat. size.

forming an intricate mass within the gelatinous envelope, generally more closely crowded towards the exterior; sheaths sometimes distinct in parts of the thallus (often near the periphery), not uncommonly yellow or brown; cells spherical, barrel-shaped, or cylindrical; heterocysts larger than, but generally of the same shape as, the vegetative cells, intercalary and terminal, often in series. Spores (not observed in all sp.) spherical or oblong, developed centrifugally in series between the heterocysts, spore-formation sometimes involving all the vegetative cells of a trichome; the young plants usually consist

[1] Ann. sci. nat., Bot., sér. 7, III, 1886, p. 323; IV, 1886, p. 343; V, 1887, p. 51; VII, 1888, p. 177.

[2] Borzi, Nuov. Giorn. Bot. Ital. X, 1878, p. 241; Geitler, Österr. Bot. Zeitschr. 1921, p. 161.

of a variously, and sometimes densely, contorted trichome within a relatively narrow, somewhat elongated, mucous investment, terminated at each end by a heterocyst. Germination of heterocysts has been observed more frequently in this genus than in any other (p. 445, fig. 182, F, G).

There are about 16 Brit. sp., some of which are much more abundant than others. *N. piscinale* Kütz., *N. coeruleum* Lyngb. (fig. 196, C), and *N. pruniforme* Ag. are widely distributed in ponds and ditches, generally occurring as free-floating masses. *N. commune* Vauch. prefers damp ground which is frequently inundated. *N. muscorum* Ag., *N. humifusum* Carm., and *N. macrosporum* Menegh. are found principally among Mosses on wet rocks. *N. sphaericum* Vauch. and *N. verrucosum* Vauch. commonly occur attached to the rocks and stones in the beds of rapid streams and rivers. The cells of *N. humifusum* are only 2–2·5 br., whereas those of *N. macrosporum* reach a diam. of 8–9. Several sp. of *Nostoc* occur in cultivated soils, but none is widespread.

No attempt has been made above to mention the differences between the sp., since in most cases that could not be done without giving a full diagnosis.

Anabaena Bory, 1822[1] (*Sphaerozyga* Agardh, 1827; *Dolichospermum* Thwaites, 1850). Trichomes straight or circinate, often destitute of all traces of a sheath, either free-floating or aggregated to form a thin mucous stratum; cells with homogeneous or granular contents, sometimes with pseudo-vacuoles, generally of uniform breadth, but trichomes sometimes slightly attenuated and with a conical apical cell; heterocysts numerous, intercalary. Spores often elongate and more or less cylindrical, sometimes solitary, sometimes in short series, either adjacent to the heterocysts (*Sphaerozyga*) or developed between them.

Although closely related to *Nostoc*, the genus *Anabaena* is easily distinguished. The vast majority of the sp. are aquatic. Even when found in a mucous stratum, which is not frequent, the latter never approaches in consistency, nor possesses the definite shape of, the tough thallus of a *Nostoc*. With one or two exceptions the trichomes of *Anabaena* are rigid and fragile and they are rarely contorted like those of *Nostoc*. The spores of the former are generally much more elongate than those of the latter.

Sp. of this genus cannot, as a rule, be kept alive very long after collection, unless placed in a large volume of water. One or two days in a small glass vessel is usually sufficient to cause disarticulation of

[1] Schmidle, Ber. Deutsch. Bot. Ges. XIV, 1896, p. 393; Fritsch, loc. cit. 1904; Spratt, loc. cit.; Smith, 1920, p. 56; Griffiths, Journ. Linn. Soc., Bot., XLVII, 1925, p. 91.

the trichomes which under these conditions often develop forms which are quite unknown in their natural state.

There are 12 Brit. sp., some of which are relatively abundant in the waters of ponds and lakes. *A. flos-aquae* (Lyngb.) Bréb. (fig. 198, E) and *A. circinalis* (Kütz.) Hansg., both with pseudo-vacuoles and much twisted trichomes, are found in the plankton of the Brit. lakes. A very characteristic member of the plankton is *A. Lemmermanni* P. Richter; here the vegetative condition is of very brief duration, and it is more customary to find the groups of heterocysts and cylindrical spores (8–11 br.; 19–33 l.) left by the disorganisation of the sporiferous trichomes. *A. oscillarioides* Bory and *A. inaequalis* (Kütz.) Born. et Flah. (fig. 197, A–D) are found among other Algae in still water; forms of both sp. have been encountered in cultivated soils. Several sp. occur among *Sphagnum* in bogs, but spores seem to be rarely developed in these situations. The trichomes vary in thickness in the different sp. from 4 to 10 μ, and the cylindrical type of spore may reach a length of 60 μ.

Aphanizomenon Morren, 1838[1]. Trichomes usually straight, slightly attenuated towards the extremities (which are composed of elongate colourless cells), with diffluent, generally invisible sheaths, agglutinated to form free-floating spindle-shaped bundles or small plates; heterocysts intercalary. Spores solitary, elongate-cylindrical, remote from the heterocysts.

A. flos-aquae (L.) Ralfs (fig. 198, A, D), the only Brit. sp., is found floating in the quiet waters of ponds and lakes, sometimes in great abundance and forming water-flowers. The rigid trichomes have subquadrate cells, cylindrical heterocysts, and are 5–6 br.; spores 60–80 l.; 7–8 br.

Fig. 197. A–D, *Anabaena inaequalis* (Kütz.) Born. et Flah., from Epping Forest, Essex. E–G, *Cylindrospermum stagnale* (Kütz.) Born. et Flah., from Ribblehead, W. Yorks. H, *Nodularia sphaerocarpa* Born. et Flah., from near Ely, Cambridgeshire. (All ×480.) *h*, heterocyst; *sp*, spore.

Nodularia Mertens, 1822. Filaments free-floating or forming a loose stratum, generally furnished with a

[1] Klebahn, Flora, LXXX, 1895, p. 271; Lemmermann, Ber. Deutsch. Bot. Ges. XVIII, 1900, p. 141.

distinct hyaline sheath, closely enveloping the trichome and sometimes becoming diffluent; trichomes more or less straight with short, depressed, often discoid cells, and usually depressed heterocysts. Spores spherical or discoidal, developed in series between the heterocysts.

The three Brit. sp. are aquatic (sometimes found in slightly brackish water). None is abundant, although *N. spumigena* Mertens, distinguished by its broad trichomes (10–15 br.), is not uncommon. *N. sphaerocarpa* Born. et Flah. (trich. 6–7 br.) (fig. 197, H) is known from Cambridgeshire.

Cylindrospermum Kützing, 1843[1]. Trichomes sometimes exhibiting movement, relatively short owing to frequent hormogone-formation, with a solitary heterocyst at one end and diffluent sheaths, mostly aggregated to form an expanded mucous stratum of indefinite shape; cells and heterocysts cylindrical, longer than broad. Spores always developed from the cell or cells adjacent to the heterocyst, generally solitary, rarely seriate, sometimes with a papillate exospore.

This genus is sharply characterised by the terminal position of heterocysts and spores. There are six Brit. sp. *C. majus* Kütz. (*C. macrospermum* Rabh., trich. 5–6 br.), with spores having a papillate membrane, is common on damp stones and earth, often forming a thin stratum on garden paths or at the edge of a pond. *C. stagnale* (Kütz.) Born. et Flah. (trich. 3·8–4·5 br.) (fig. 197, E–G) is not uncommon in boggy ditches, particularly in peaty ones. *C. catenatum* Ralfs, with spores in series, is much rarer, occurring on the damp mud of stagnant rivers and ditches. Various sp. are found in cultivated soils, but none is common.

Family 3. SCYTONEMATACEAE

The majority of the members of this family are sharply characterised by the production of false branches, the possession of heterocysts, and the usually firm texture of the sheaths. Except in the rare genera *Desmonema* (fig. 200, B), *Hydrocoryne*, and *Diplocolon* (fig. 200, A), there is always only a single trichome within the sheath which is strong, tubular, and of practically uniform thickness; it may be homogeneous and colourless, or lamellose and of a yellow or brown colour. The trichomes of the main filament break at intervals[2] and perforate the sheath, growing out as long flexuose branches which develop a sheath of their own. These pseudo-branches arise either singly

[1] Glade, Cohn's Beitr. z. Biol. d. Pfl. XII, 1914, p. 295.

[2] This may be due to the dying away of a cell or (in *Tolypothrix*) to the formation of heterocysts.

or in pairs; in the latter case they sometimes originate as a loop-like outgrowth which subsequently breaks across at the apex. The trichomes are cylindrical, but towards the growing end of the filament they often increase in diameter, the cells becoming much shorter and more rounded. Heterocysts are lacking only in *Plectonema* (fig. 198, C). The normal method of reproduction is by hormogones which are formed at the ends of the branches

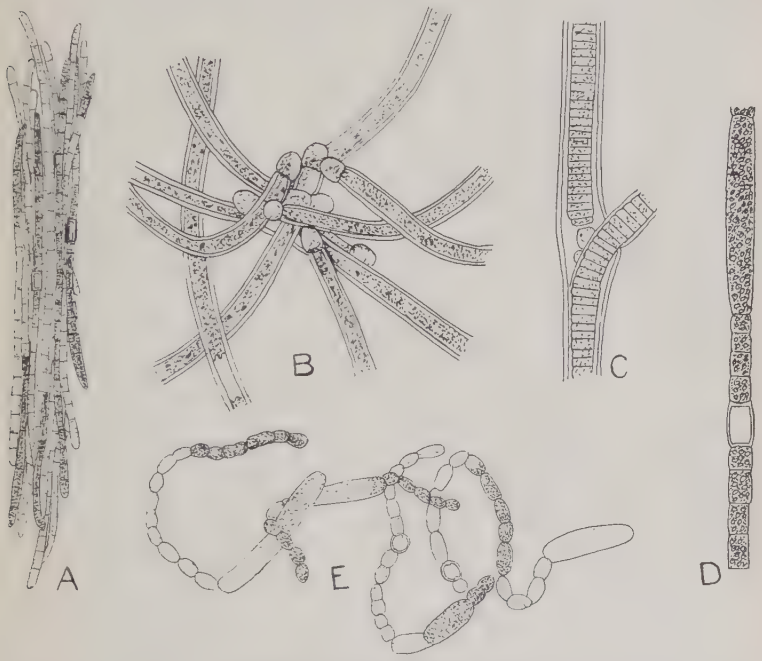

Fig. 198. A and D, *Aphanizomenon flos-aquae* (L.) Ralfs (after G. M. Smith); A, stratum (×280); D, single trichome (×700). B, *Microchaete tenera* Thur. (after Bornet, ×465). C, *Plectonema Tomasinianum* (Kütz.) Born. (after Bornet & Thuret). E, *Anabaena flos-aquae* (Lyngb.) Bréb. (after G. M. Smith, ×280).

and gradually emerge from the sheath. Ellipsoidal or globular spores are occasionally produced in most genera.

Plectonema Thuret, 1875. Filaments in free-floating caespitose masses, or densely interwoven to form felts or mats amongst damp Mosses and on wet rocks; sheaths firm, rather thin, sometimes lamellose, hyaline or rarely yellow-brown; false branches frequent, usually in pairs, the two branches directed to the same side or not. Trichomes fitting closely within the sheaths, often slightly constricted between the cells; heterocysts absent.

This genus has often been placed amongst the Oscillatoriaceae; the only marked difference from *Scytonema*, however, lies in the absence of heterocysts. Of the three Brit. sp., *P. Tomasinianum* (Kütz.) Born. (fil. 16–27; trich. 12·5–22 br.; cells 3–9 l.) (fig. 198, C) is the largest and most frequent, occurring as greenish-brown felt-like masses on wet rocks. Thick-walled resting cells, probably of the nature of spores, have been observed in this sp.[1] *P. Battersii* Gom., a sp. hitherto thought to be purely marine, has been shown to be a common constituent of the algal flora of cultivated soils (Bristol, 1920, p. 50); it has narrow trichomes (2–3·5 br.) and the elongate false branches are thinner than the main axes.

Microchaete Thuret, 1875[2]. (*Coleospermum* Kirchner, 1878.) Filaments without branches, or pseudo-branches very exceptional, fixed at the base, erect and solitary, or forming radiating tufts (fig. 198, B), or tortuose-flexuose and forming a soft felt; trichomes with a prominent tough sheath, sometimes somewhat attenuated. Heterocysts basal, or basal and intercalary. Spores cylindrical, usually solitary, near the basal heterocysts or remote from them. Baumgaertel (loc. cit.) has described the budding off of "gonidia" from the ends of the trichomes of *M. calotrichoides* Hansg.

Kirchner[3] referred this genus to Nostocaceae, but the plants are much like unbranched specimens of *Scytonema*, which they also resemble in the occasional possession of thick growing apices with shorter cells. Geitler (1925, p. 278) places the genus in a special family, the Microchaetaceae, characterised by the unbranched filaments and the possession of heterocysts, and to this family he also refers *Desmonema* (p. 484). One may well await a better knowledge of these genera before agreeing to this step.

Sp. of *Microchaete* are in part marine and are very rarely met with. *M. diplosiphon* Gom. var. *Cumbrica* West is known from the English Lake District; the species has a double sheath, of which the outer is very mucilaginous (23–30 br.) and the inner thin but firm (6·5–9 br.).

Scytonema Agardh, 1824. (*Petalonema* Berkeley, 1833[4]; *Schizosiphon* Kützing, 1843 (in part); *Symphyosiphon* Kützing, 1843 (in part); *Arthrosiphon* Kützing, 1845.) Filaments generally forming a dense intricate mass on damp or wet substrata, more rarely submerged, more or less abundantly provided with false branches; the latter are usually in pairs, though occasional solitary ones are mostly to be found, but the branches nearly

[1] West, 1904, p. 333.
[2] Baumgaertel, Ber. Deutsch. Bot. Ges. xxxv, 1917, p. 537.
[3] Engler and Prantl, Nat. Pflanzenfam. I Teil, Abt. I *a*, 1900, p. 76.
[4] Both Lemmermann (1910, p. 214) and Geitler (1925, p. 261) maintain *Petalonema* as a genus distinct from *Scytonema*.

always arise remote from the heterocysts. Sheath tough, lamellose, of a golden-yellow or brown colour, the strata of the sheath either parallel or more or less divergent, their edges in the latter case sometimes projecting and producing a frayed margin (so-called *ocrea*). Heterocysts intercalary, like the vegetative cells of variable shape. Spherical or ovoid spores known in a number of sp.

There are about eight Brit. sp., the majority of which are terrestrial. *S. crispum* (C. A. Ag.) Bornet (*S. cincinnatum* (Kütz.) Thur.), with scantily branched filaments (18–36 br.; trich. 14–30 br.; cells usually much shorter than they are long), is found in ponds and streams.

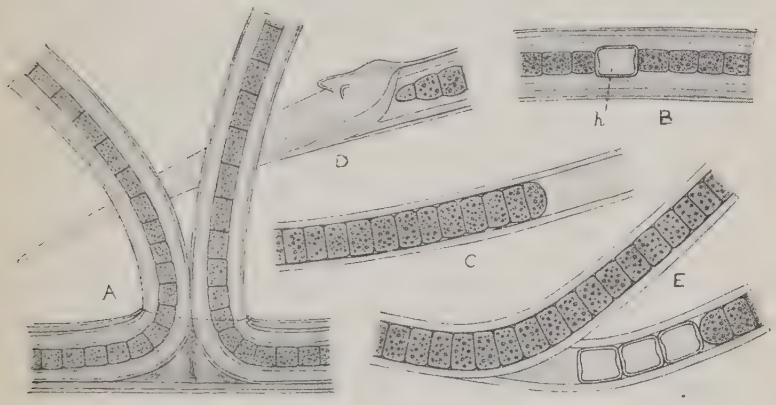

Fig. 199. A–D, *Scytonema mirabile* (Dillw.) Born., from Cronkley Fell, N. Yorks (×440); C, apex of a "branch"; D, organ of attachment at base of filament. E, *Tolypothrix lanata* (Desv.) Wartm., from Riccall Common, E. Yorks (×440). *h*, heterocyst.

S. Myochrous Ag. and *S. mirabile* (Dillw.) Born. (*S. figuratum* Ag., fil. 15–21 br.) (fig. 199, A–D) are the two most abundant of the Brit. terrestrial sp., the former often occurring on wet rocks as large felt-like masses an inch thick; both sp. have sheaths with divergent strata, but this feature is much more pronounced in *S. Myochrous* which also has much thicker filaments (18–36 br.; trich. 6–12 br.). *S. alatum* (Berk.) Borzi (*Petalonema alatum* Berk.)[1] is frequent on wet rocks of carboniferous limestone forming a brownish-green stratum thickly encrusted with lime; the filaments (24–66 br.; trich. 9–15 br.) have very wide sheaths, with prominently diverging strata. Some sp. of *Scytonema* are the algal components of Lichens.

[1] Both Lemmermann (1910, p. 214) and Geitler (1925, p. 261) maintain *Petalonema* as a genus distinct from *Scytonema*.

Tolypothrix Kützing, 1843 (incl. *Hassallia* Berkeley, 1845). Filaments forming a floccose floating mass, or submerged tufts, or more rarely a stratum on damp rocks, etc.; false branches more or less frequent, usually single and mostly issuing from the main filament beneath one or more heterocysts. Sheaths usually thinner than those of *Scytonema*, colourless or yellow to brown, either flexible or more or less fragile[1]. Heterocysts sometimes 3-, 4-, or 5-seriate. Hormogones formed at the ends of the filaments. Spores spherical, oval, or ellipsoid, singly or in series.

Tolypothrix is closely allied to *Scytonema* and there are no doubt intermediate forms in which the branching peculiar to each genus is combined; at the same time the majority of the sp. are distinguished without difficulty. On the whole the two genera differ in habitat, *Scytonema* being essentially terrestrial and *Tolypothrix* chiefly aquatic, and this is reflected in the characters of the sheaths. Of the four Brit. sp., the most frequent are *T. lanata* (Desv.) Wartm. (fil. 9–12·5 br.; trich. 7·5–10 br.) (fig. 199, E) and *T. tenuis* Kütz. (fil. 8–10 br.; trich. 6–8 br.), which occur amongst various aquatic plants in ponds and lakes.

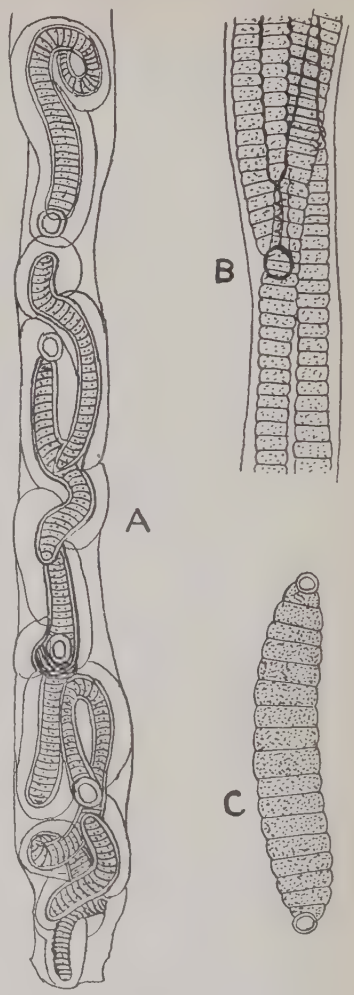

Fig. 200. A, *Diplocolon Heppii* Naeg. (after Itzigsohn, ×250). B, *Desmonema Wrangelii* (Ag.) Born. & Flah. (after Borzi, ×270). C, *Stigonema ocellatum* (Dillw.) Thur., hormogone (after West, ×520).

Desmonema Berkeley and Thwaites, 1849[2]. Filaments

[1] This, the only character separating *Hassallia* from *Tolypothrix*, is quite inadequate as a generic distinction.

[2] Borzi, Nuov. Giorn. Bot. Ital. XI, 1879, p. 348. The affinities of this genus are quite unclear; cf. also under *Microchaete*.

forming penicillate tufts, submerged, sometimes slightly branched in a dichotomous manner; each fil. with two or more trichomes which are slightly attenuated at either end. Heterocysts solitary, only at the base of the trichomes. Spores ovoid or ellipsoid, singly or in series.

D. Wrangelii (Ag.) Born. & Flah. (trich. 9–10 br.) (fig. 200, B) is a very rare Brit. Alga forming penicillate tufts, 5–6 mm. high, on stones in streams and waterfalls.

Diplocolon Naegeli, 1857[1]. Filaments branched like those of *Scytonema*, but the pseudo-branches much shorter and greatly contorted; each trichome has a special sheath of its own and several filaments, with their branches, are included within a wider common envelope. Heterocysts intercalary or basal. Spores unknown.

D. Heppii Naeg. (fil. 20–28 br.; trich. 6–10 br.) (fig. 200, A) has been found in Yorkshire forming a brownish-green gelatinous stratum on damp calcareous rocks.

Family 4. RIVULARIACEAE

The chief characteristic of this well-marked family is to be found in the more or less gradual attenuation of the trichomes which terminate either in a point (some sp. of *Calothrix* (fig. 201, B)) or much more usually in a hair composed of elongate colourless cells (fig. 203, C). At the broad basal end of the trichome, in all except a few genera (e.g. *Amphithrix* (fig. 203, B)), one or two heterocysts are located; in some cases (*Calothrix*) intercalary heterocysts occur in addition to the basal ones. The trichomes possess tubular sheaths, but in some species the basal heterocysts are not included within these sheaths. The latter are either gelatinous, or more often firm and membranous, and then usually distinctly lamellose. In some species the lamellae of the sheath become dilated upwards, giving the exterior of the filament a fimbriate appearance (fig. 201, A, B). It frequently happens that the sheaths of adjacent filaments become fused to such an extent that their individuality is lost. The mature sheaths are usually yellow or yellowish-brown and in some cases they are indurated with carbonate of lime.

The filaments nearly always exhibit false branching, due to the outgrowth of some of the inferior cells of the trichomes; frequently this takes place beneath an intercalary heterocyst, the branch continuing growth in the direction of the main trichome, the upper part of which is turned aside and appears as the

[1] Itzigsohn, Nov. Act. Leop.-Carol. xxvi, 1858, p. 160.

"branch." If this happens again and again, a sympodial construction is obtained. Branching is clearly evident in such genera as *Calothrix* and *Dichothrix* (cf. also fig. 202, E), but in other cases owing to abundant production of mucilage the "branches" become displaced sooner or later (*Rivularia*, *Gloeotrichia*); it is in this way that the globose colonies of *Rivularia* and *Gloeotrichia* originate.

Hormogones are formed from the upper parts of the trichomes, the apical hair being shed. In germination the hormogone frequently becomes attenuated at each end, a condition that persists in *Hammatoidea* (fig. 204), but in other cases the young thread breaks across at its middle where two heterocysts are originating and two normal trichomes are thus produced. In many cases the growth of the trichomes is trichothallic, the cells below the terminal hair constituting the meristematic region which also produces the hormogones. Spores occur in *Gloeotrichia* (fig. 203, A) and *Calothrix*, arising close to the basal heterocysts.

Algae of this family are fairly abundant in mountainous districts and also occur sparingly in the less elevated parts of the country. They are found principally on the dripping rocks of waterfalls, cataracts, and streams, or at the margins of rocky lakes. They form soft felt-like expanses, or hard hemispherical masses, generally of a brown colour, but a few of them occur as blue-green nodules attached to the stems and leaves of submerged plants. They are not often found in the plankton.

Amphithrix Kützing, 1843; emend. Bornet & Flahault, 1886. Filaments forming a thin expanded purple or violet stratum, the inferior layer of which is composed of densely intricate threads forming a kind of parenchymatous disc, or of minute radiately disposed series of cells, whilst the superior layer consists of simple erect filaments closely packed together and attenuated to fine points; sheaths thin and close. Heterocysts absent.

A. janthina (Mont.) Born. & Flah., the only Brit. sp., occurs on wet rocks and is known from W. Yorks; fil. 1·5–2·25 br. (fig. 203, B). It is very imperfectly known.

Calothrix Agardh, 1824. (*Mastigothrix* Kützing, 1843; *Schizosiphon* Kützing, 1843 (in part); *Symphyosiphon* Kützing, 1843 (in part); *Homoeothrix* (Thuret) Kirchner, 1900.)[1] Filaments simple or with scanty false branches, sometimes solitary, more usually forming penicillate tufts or soft velvety expansions which are generally attached to submerged rocks and stones, some sp. epiphytic; sheaths firm, often brown, frequently thick and lamellose, often diffluent in the upper portion; trichomes

[1] Borzi, Nuov. Giorn. Bot. Ital. xiv, 1882, p. 274.

sometimes long and flexuous, ending in a point or in a long hair. Heterocysts basal and (rarely) intercalary, absent in a few sp. (*Homoeothrix*)[1]. Spores, formed singly or in series adjacent to the basal heterocysts, are known only in a few sp. Hormogones often formed in series.

Fig. 201. A and B, *Calothrix parietina* (Naeg.) Thur., from Arncliffe, W. Yorks. C, *Dichothrix interrupta* W. & G. S. West, from Slieve Donard, Ireland. D, *D. Orsiniana* (Kütz.) Born. & Flah., from Langdale, Westmorland. *h*, heterocysts. (All ×420.)

There are about six Brit. freshwater sp., *C. parietina* (Naeg.) Thur. (trich. 6–12 br.) (fig. 201, A and B) being the most frequent. *C. fusca* (Kütz.) Born. & Flah., in which the trichomes are prominently swollen at the base, and *C. epiphytica* W. & G. S. West, with colourless sheaths, and trichomes merely terminating in a point, are epiphytes on other larger Algae, such as *Vaucheria* or *Batrachospermum*.

Dichothrix Zanardini, 1858. Filaments more or less abundantly branched in a dichotomous manner, generally forming penicillate tufts, each filament including two to several trichomes enveloped

[1] The genus *Homoeothrix*, distinguished by the absence of heterocysts, is upheld by many authorities.

by sheaths of their own and really representing a branch-system; the trichomes produce large numbers of false branches, some of which remain included with the main trichome in a common sheath, whilst others stand off freely either at once or only in the upper part of their course. Heterocysts basal or intercalary, absent in one sp. Spores unknown.

This genus really only differs from *Calothrix* in the inclusion of several branch-trichomes within a common sheath. The five Brit. sp. are all rare and occur principally on dripping rocks in mountainous regions. *D. Nordstedtii* Born. & Flah. and *D. Orsiniana* (Kütz.) Born. & Flah. (fil. 10–14 br.; trich. 6–7·5 br.) (fig. 201, D) are widely distributed, whilst *D. interrupta* W. & G. S. West (fig. 201, C) is known from the Mourne Mts., Down, Ireland[1].

Rivularia (Roth) Agardh, 1824 (in part); emend. Thuret, 1885. (*Zonatrichia* J. Agardh, 1842; *Limnactis* Kützing, 1843; *Schizo-*

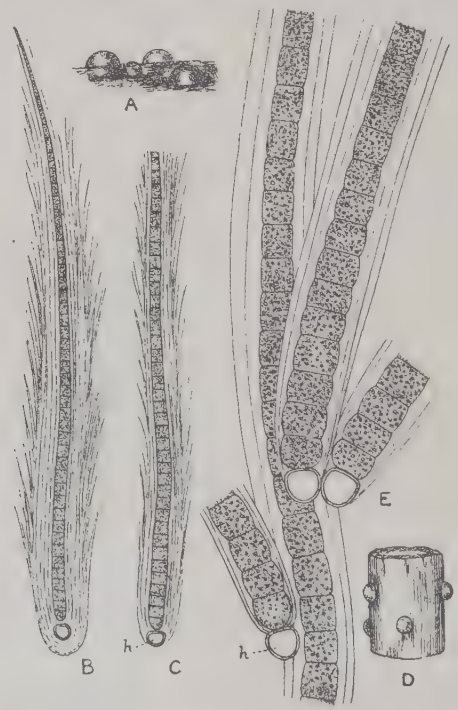

Fig. 202. A–C, *Rivularia Biasolettiana* Menegh., from Arncliffe, W. Yorks; A, nat. size, on surface of stone; B and C, ×480. D and E, *R. minutula* (Kütz.) Born. & Flah., from Chippenham Fen, Cambridge; D, nat. size, on stem of *Phragmites*; E, ×480. *h*, heterocysts.

[1] cf. West, Journ. Roy. Microscop. Soc., 2 ser. XIV, 1894, p. 16.

siphon Kützing, 1843 (in part).) Thallus macroscopic, composed of a globose, hemispherical, or irregular tough gelatinous mass attached to submerged plants (fig. 202, D) or stones, and containing numerous radiating filaments which are repeatedly "branched," a fact which is only obvious in relatively young colonies: sheaths of the individual filaments often diffluent. Thallus sometimes showing deposition of lime within the mucilage and this may lead to the formation of hard calcareous masses containing living trichomes only in their outer parts. Trichomes piliferous; heterocysts basal, or intercalary at points of branching. Spores unknown.

Of the four Brit. freshwater sp., *R. haematites* (DC.) Ag. (*Zonatrichia calcarea* (Eng. Bot.) Endl.) is the most frequent, sometimes occurring in quantity attached to the stones of mountain streams in limestone districts; this sp. forms strata which are often completely indurated with lime. *R. dura* Roth, with hard thalli in which the individual trichomes (4–9 br.) are not easily separated by pressure, and *R. minutula* (Kütz.) Born. & Flah.[1] (trich. 2–12·5 br.) (fig. 202, D and E) are occasionally met with on submerged plants (*Chara*, *Myriophyllum*, or bases of stems of *Phragmites*) as small globose masses of a blue-green or greenish-black colour. Some sp. of *Rivularia* are marine.

Gloeotrichia J. Agardh, 1842. Thallus soft, globose, at first attached, later often free-floating, solid when young, but inflated

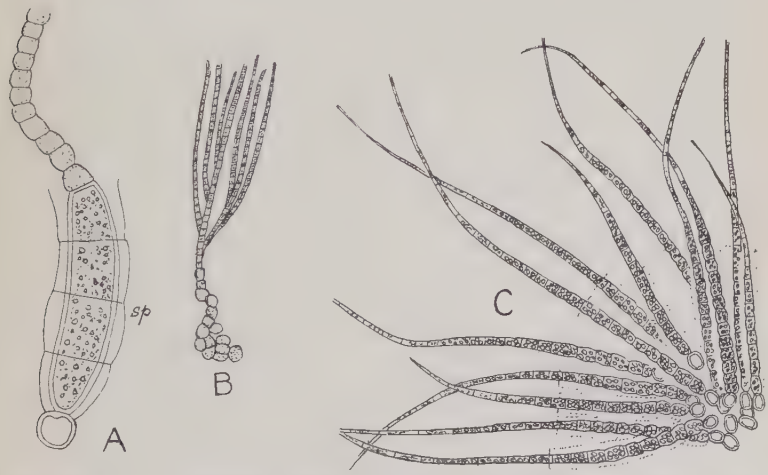

Fig. 203. A, *Gloeotrichia natans* (Hedw.) Rabenh. (after Tilden), with spore (*sp*). B, *Amphithrix janthina* (Mont.) Born. & Flah. (after Kirchner, ×345). C, *Gloeotrichia echinulata* P. Richt. (after G. M. Smith, ×240).

[1] Various recent authorities (Lemmermann, Geitler) regard this species as synonymous with *R. Biasolettiana* Menegh.

and hollow when old; filaments radiating from centre outwards, falsely "branched" as in *Rivularia*; sheaths only conspicuous near the bases of the trichomes (fig. 203, C), being gelatinous and confluent in the outer parts of the thallus; trichomes strongly attenuated from the base, more or less torulose. Elongated cylindrical spores are developed from the cell immediately above the heterocyst and remain for some time within the basal part of the sheath (fig. 203, A) which at this stage is often yellow or brown; the sporiferous colonies generally break up sooner or later and the trichomes involved frequently shed their apical portions.

This genus is distinguished from *Rivularia* only by the customary development of spores and the frequent free-floating habit; its maintenance is purely a matter of convenience. There are three Brit. freshwater sp. *G. Pisum* (Ag.) Thur. and *G. natans* (Hedw.) Rabenh. (fig. 203, A) are common; the former possesses a thallus which does not exceed 2 mm. in diameter, but the latter is a larger form whose thallus may reach 10 cms. *G. Pisum* is often concerned in the phenomenon of the "breaking of the meres." *G. echinulata* P. Richt. (fig. 203, C), in which the trichomes project at the surface of the colony, is known from the plankton of the Scotch lakes.

Hammatoidea W. & G. S. West, 1897[1]. Filaments epiphytic, exhibiting false branching, suddenly bent in their median widest portion, the two more or less parallel extremities being gradually attenuated to piliferous apices; the "branches" show the same form as the main filaments. Sheaths firm and lamellose, colourless in young, but yellow-brown in older filaments; trichomes exhibiting slight constriction between the median cells, the

Fig. 204. *Hammatoidea Normanii* W. & G. S. West, from Dartmoor, Devonshire (×420).

[1] Journ. Roy. Microscop. Soc. 1897, p. 506; Bachmann, Mitteil. Naturf. Ges. Luzern, VIII, 1921, p. 16. This genus was first described under the name of "*Ammatoidea*."

apical cells about six times longer than their diameter. Heterocysts absent. Hormogonia formed from the median parts of the trichomes. Spores unknown.

This genus was referred by West (loc. cit. and 1904, p. 341) to the family of the Camptotrichaceae. There can be no doubt, however, that *Hammatoidea* is closely allied to some of the Rivulariaceae which produce hormogonia tapering towards both extremities (cf. p. 486 and Geitler, 1925, p. 212).

H. Normanii W. & G. S. West (fig. 204) is recorded from Dartmoor as an epiphyte on *Batrachospermum moniliforme*; fil. 5·5–12·5; trich. 3·5–5·5 br.

Family 5. STIGONEMATACEAE

This is the only British family[1] of Hormogoneales in which true branching is found, the branches originating either by the putting out of a protuberance from a cell of the main trichome or arising by the outgrowth of one half of a cell subsequent to a longitudinal division. Branching is usually abundant and there is commonly a marked distinction between main axes and laterals. In some genera (*Hapalosiphon* (fig. 205)) the cells are arranged in a single series, but in *Stigonema* (fig. 206) there are usually two or more irregular series of more or less rounded cells which are provided with close-fitting sheaths of their own and are usually connected by very obvious protoplasmic processes (fig. 206, D). In *Hapalosiphon* the sheaths of the filaments are generally thin and regular, but in *Stigonema* they are mostly thick, dark brown in colour, of considerable toughness, and with a very uneven exterior. The filaments increase in length by the division of the cells towards the apices. The heterocysts are either intercalary, being scattered at intervals between the vegetative cells or, when more than one row of cells is present, they are lateral in position (fig. 206, C); in *Nostochopsis*[2] the heterocysts are in part seated on short stalks. Reproduction is effected by hormogones (fig. 200, C) which are formed in the branches, and by spores. The Stigonemataceae appear to represent the highest development among the Myxophyceae.

Only two genera of this family have so far been recorded in the British Isles and these, *Hapalosiphon* and *Stigonema*,

[1] Geitler (1925, p. 165, and Beih. Bot. Centralbl. xli, 1925, Abt. ii, p. 252) has recently undertaken a revision of the genera referred to Stigonemataceae, grouping them as Stigonematales and classing them in six families, of which the Stigonemataceae with *Stigonema* and *Hapalosiphon* and other genera form one.

[2] Placed in a separate family by Geitler, loc. cit.

represent two extremes whose chief common characteristic lies in the presence of true branches.

Hapalosiphon Naegeli, 1849[1]. Filaments free-floating amongst other Algae or rarely subaerial in moist situations; primary filaments never very thick, consisting of a single row (rarely of two rows) of cells enclosed within a strong sheath of uniform thickness; branches usually not branched to the second degree, sometimes as thick as the primary filaments, more often slightly narrower, few and distant or occasionally in clusters, commonly unilateral, mostly long and flexuose and very slightly attenuated, with thinner, generally quite colourless, sheaths; cells of branches proportionately much longer than those of the primary filament, those of the latter opposite the base of a branch usually projecting into it. Heterocysts intercalary. Spores not uncommon, with thick yellowish-brown walls, the majority (or even all) of the cells of certain portions of a plant sometimes becoming converted into spores (fig. 205, E).

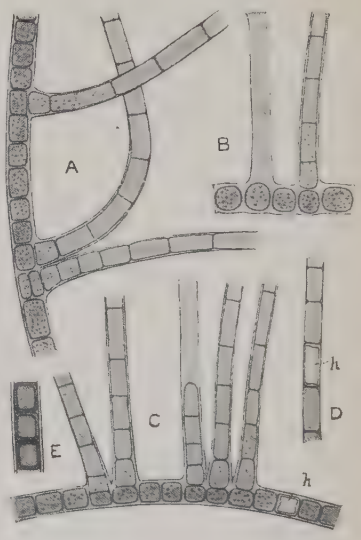

Fig. 205. *Hapalosiphon hibernicus* W. & G. S. West, from Glen Caragh, Kerry, Ireland (×440). E, portion of a row of spores within the sheath. *h*, heterocysts.

In contrast to *Stigonema* this genus is essentially aquatic in habit. The Brit. sp. are most frequently met with amongst *Utricularia minor* and submerged *Sphagnum*. The two most widely distributed are *H. intricatus* West (fil. 4–7 br.), in which the branches are of about the same width as the main filaments, and *H. hibernicus* W. & G. S. West (fil. 6–10 br.) (fig. 205).

Stigonema Agardh, 1824[2]. (*Sirosiphon* Kützing, 1843.) Filaments free-floating or more commonly aggregated to form soft felt-like or cushion-like masses on damp surfaces; filaments frequently very wide, irregular, and often richly provided with short, thick, irregularly disposed branches; cells always rounded,

[1] W. and G. S. West, Journ. of Bot. xxxv, 1897, p. 241.
[2] Hieronymus, Hedwigia, xxxiv, 1895, p. 154.

with obvious protoplasmic connections and usually with distinct sheaths of their own, mostly disposed in two or more rows (rarely one) within a thick lamellose, generally golden-yellow or brown sheath which often has an uneven exterior; branches often considerably narrower than the main filaments. Heterocysts commonly lateral or less frequently intercalary. Reproduction normally by hormogones formed from the ends of the branches and often few-celled (fig. 200, C).

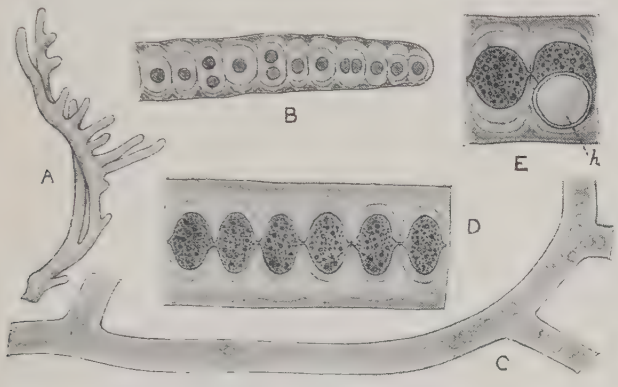

Fig. 206. A and B, *Stigonema minutum* Hass., from Slieve Donard, Down, Ireland; A, ×100; B, ×440. C–E, *S. ocellatum* (Dillw.) Thur., from Llyn Teyrn, Snowdon, N. Wales; C, ×100; D and E, ×440. *h*, heterocyst.

Sp. of this genus occur principally on damp or wet rocks, but are sometimes observed free-floating in ponds and lakes. Of the seven Brit. sp., *S. hormoides* (Kütz.) Born. & Flah. is the smallest (fil. 7–15 br.) and has the cells arranged in a single series; this is also the case in *S. ocellatum* (Dillw.) Thur. (fig. 206, C–E), in which however the filaments are much wider (14–50 br.). The largest sp. are *S. informe* Kütz. (fil. 40–70 br.), with gelatinous sheaths, and *S. mammillosum* Ag. (fil. up to 90 br.), with firm sheaths; according to Geitler (1925, p. 189) the latter grows by means of an apical cell. Sp. of *Stigonema* are the algal constituents of a number of Lichens.

Genera incertae sedis

Glaucocystis Itzigsohn, 1854[1]. Cells often (always?) somewhat zygomorphic, with a prominent colourless area occupying the median part of the elliptical front-view; side-view obliquely elliptical, one margin more strongly curved than the other; cross-section ovate, the colourless area at the pointed end.

[1] Griffiths, Ann. of Bot. xxix, 1915, p. 423; Chodat, Bull. Soc. Bot. Genève, xi, 1919, p. 42; Geitler, Archiv f. Protistenkunde, xlvii, 1923, p. 1.

Nucleus (fig. 207, C, *n*) large, spherical or ellipsoidal, central, well-defined[1]; chromats. a number of curved blue-green bands grouped in a radiating manner (fig. 207, D) about the nucleus (but lacking in the region of the colourless area) and breaking up into a number of short rods (fig. 207, C) when the cells commence to divide; cell-wall mainly composed of cellulose, commonly with polar thickenings at either end and often with an equatorial thickening; starch-grains and drops of fat present in cytoplasm. Reprod. by division of the protoplast, successively or simultaneously, to form two, four, or eight daughter-cells which acquire membranes of their own and may remain enclosed for a time within the enlarged wall of the parent-cell (fig. 207, D).

This puzzling genus has in recent years been investigated by Griffiths, Chodat, and Geitler (loc. cit.). Opinions have differed widely as to its systematic position; G. S. West[2] and others have regarded it as a member of the Myxophyceae distinguished by its high cellular differentiation, others (e.g. Brunnthaler[3]) have advocated a reference to the Oocystaceae (p. 122), whilst Chodat (loc. cit.), owing to the asymmetry of the cell, the large nucleus, the rod-shaped chromatophores, etc. has referred it to the Peridinieae (cf. also Oltmanns, 1922, p. 70). Quite recently Geitler (loc. cit. p. 9) interprets it as a colourless form inhabited by symbiotic Blue-green Algae which constitute the chromatophores; according to him the latter are differentiated into a peripheral coloured and a colourless central region which takes on a deep stain with methylene blue. Before such a view can find acceptance, it will be necessary to cultivate the blue-green "symbiont" separately and to show that it is capable of leading an independent existence.

G. Nostochinearum Itzigs. (cells 30–45 l.; 18–25 br.) (fig. 207, C, D) is somewhat scarce, but widely distributed throughout the Brit. Islands. It is found chiefly among submerged *Sphagnum*.

Gloeochaete Lagerheim, 1883[4]. (*Schrammia* Dangeard, 1889.) Cells enveloped in a wide mucous coat, isolated or in twos or fours (fig. 207, B), attached to aquatics, subglobose, dorsi-ventral; in side-view (fig. 207, A) the margin of the cell next to the substratum is seen to be rounded, whilst the opposite one is slightly hollowed out; adjacent to the latter is a prominent zone of colourless cytoplasm containing a contractile vacuole (*cv*), whilst the rest of the protoplast is deeply pigmented, appearing as a bell-shaped chromatophore, but according to Geitler (loc. cit. p. 14) actually comprising a large number

[1] cf. however Griffiths, loc. cit. p. 425.

[2] West, 1904, p. 317; cf. however West, 1916 *a*, p. 40.

[3] Verhandl. Zool.-Bot. Ges. Wien, 1913, p. 88.

[4] Lagerheim, Nuova Notarisia, 1, 1890, p. 227; Geitler, loc. cit. 1923, p. 13.

of slightly curved scattered rod-shaped chromatophores (*p*). Nucleus large, central; rod-shaped starch-grains and fat-bodies present. Each cell is furnished on its outer surface with one or two long thin bristles which sometimes give off small branches or spurs near their apices; according to Geitler the bristles consist of a central prolongation of the cytoplasm enveloped by colourless mucilage which thins out towards the apex. Multiplication of cells by division; reproduction unknown (Dangeard[1] has reported zoospores, which are very doubtful).

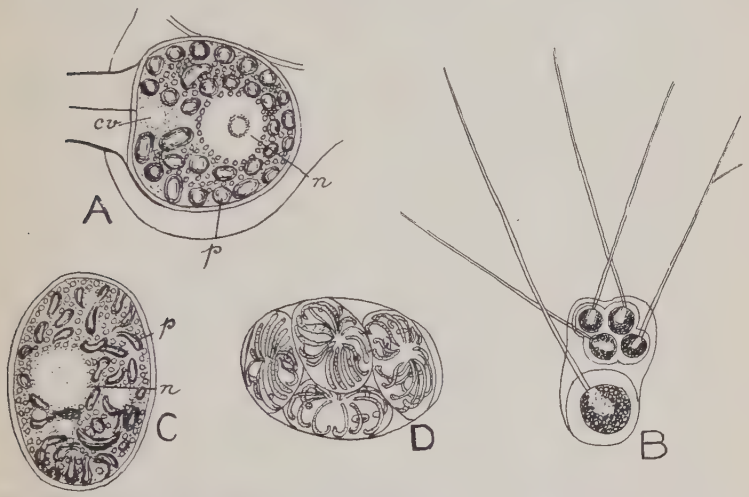

Fig. 207. A–B, *Gloeochaete Wittrockiana* Lagerh.; A, single cell (after Geitler, ×1125); B, from Pilmoor, N. Yorks (×312). C–D, *Glaucocystis Nostochinearum* Itzigs.; C, single cell (after Geitler, ×675); D, 4-celled colony (after Hieronymus). *cv*, contractile vacuole; *n*, nucleus; *p*, chromatophore.

This genus has been regarded as a highly differentiated member of the Chroococcaceae (West, 1916 *a*, p. 40), as one of the Chaetopeltidaceae (Wille, 1909, p. 102), and as a close ally of *Glaucocystis*. Geitler (loc. cit.) has recently advanced the same view as to its nature as he has propounded for *Glaucocystis*. It is not perhaps quite certain that all the different investigators have had the same Alga before them.

G. Wittrockiana Lagerh. (fig. 207, A, B) is known from several parts of the Brit. Islands as an epiphyte on *Vaucheria*, *Cladophora*, or the leaves of *Sphagnum*; cells 6–21 br.; bristles 96–260 l. A second form, *G. bicornis* Kirchn., has a pair of bristles attached to each cell, but according to Geitler this is a character that merely depends on the age of the cell.

[1] Dangeard, Le Botaniste, 1, 1889, p. 160.

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(The following list comprises a number of works to which frequent reference is made in the preceding pages and which are quoted merely by citing the name of the author and the year. It must not be assumed that the papers below enumerated are necessarily more important than others mentioned in the main body of the work, nor do they represent a definite bibliography for any part of the subject-matter.)

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ADDENDA

Since the completion of the manuscript, Mr D. J. Scourfield has drawn the writer's attention to the plentiful occurrence of a form resembling *Chlorochromatium aggregatum* Lauterb.[1] in a pond in Epping Forest. This organism consists of greenish rod-shaped cells, a number of which are closely aggregated around a central elongate colourless body. The latter is believed to be one of the Bacteria, while the former are suspected of being symbiotic Myxophyceae. The aggregate, which measures 8–12 by 5–7 μ is motile and, in material

[1] Cf. Buder, Ber. Deutsch. Bot. Ges. xxxi, 1913, p. (80); Lauterborn, Allgem. Bot. Zeitsch. xix, 1913, p. 97; Geitler and Pascher, Süsswasserflora, xii, 1925, p. 460.

described from the continent, the central organism has been found to possess an apical flagellum. It is not unlikely that such symbiotic communities are rather common, but they are easily overlooked on account of their minute dimensions.

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All measurements, except where otherwise stated, are given in terms of μ (one-thousandth of a millimetre). The following abbreviations are used in the text: aplanosp. = aplanospore; aquat. = aquatic; asex. = asexual; auxosp. = auxospore; azygosp. = azygospore; br. = breadth; Brit. = British; chloropl. = chloroplast; chromat. = chromatophore; conjug. = conjugation; contr. vac. = contractile vacuole; diam. = diameter; div. = division; fil. = filament; intercell. sp. = intercellular spaces; l. = length; longit. = longitudinal; multipl. = multiplication; opp. = opposite; pyren. = pyrenoid; reprod. = reproduction; sex. = sexual; sp. = species; terrestr. = terrestrial; transv. = transverse; trich. = trichome; unicell. = unicellular; vac. = vacuole; zoosp. = zoospore; zygosp. = zygospore.

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